NUTRITIONAL AND BEHAVIORAL ASPECTS OF REPRODUCTION IN WALRUSES

GEHNRICH

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NUTRITIONAL AND BEHAVIORAL ASPECTS OF REPRODUCTION IN WALRUSES

A

THESIS

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ABSTRACT

Walruses (Odobenus rosmarus) at Marineland, California consumed food in increasing amounts as they grew larger but ate less per unit of body weight. Adult males consumed the most food in November - December, then fasted throughout the breeding season. Females apparently fasted during ovulation and birth. Females consumed 50% more energy while pregnant or lactating than when not pregnant or lactating.

Male walruses spent more time displaying, and their displays were more stereotyped, during the breeding season. Females initiated and terminated interactions with the males during the breeding season, and those interactions were preceeded by displays. Females vocalized to the calf to initiate suckling bouts, reassure the calf. and to call the calf. Calves vocalized to initiate suckling bouts and indicate danger. When the calf was threatened, the female responded quickly by tusk strikes, kinesic tusk threats, vocal threats, or calling the calf. The calf tended to follow the female.

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INTRODUCTION

Walruses (Odobenus rosmarus) spend most of their lives in association with the arctic pack ice. Because walruses under natural conditions are far from shore in ice-covered arctic waters throughout most of the year, the study of their behavior is difficult and few data have been gathered. In addition, wild walruses tend to haul out in large groups and to return to the water periodically to feed. For those reasons, continual observation of the same individuals for even a few days at a time usually is not feasible in the wild.

Before 1960, most behavioral information on walruses was collected as a byproduct of other kinds of studies. Since then, general behavior on terrestrial and ice haulouts has been described (Miller 1976, 1982; Miller and Boness 1983; Salter 1978, 1979, 1980; Bel'kovich and Yablokov 1961), and threat behavior has been examined (Miller 1975b, 1982). Thermoregulatory behavior (Fay and Ray 1968), responses to disturbance (Loughrey 1959; Salter 1978, 1979) and reproductive behavior, including vocalizations, also have been studied (Schevill et al. 1966; Ray and Watkins 1975; Fay and Ray 1979; Stirling et al. 1982; Fay, Ray and Kibal'chich 1984).

These studies have raised several questions concerning the survival strategy of the walrus, which has a life history pattern typical of a large mammal (Stearns 1976). Walruses develop slowly, grow to a large size, delay reproduction, are iteroparous, care for their young for a long time, and have high survival rates (Harrison 1969; Fay

1982). It would seem that this survival strategy would rely on well evolved behavioral systems, especially those related to reproductive behavior, parental care and feeding.

The purpose of this study has been to examine these behavioral systems by defining the energy demands of walruses in relation to sex, age, season, and reproductive status and by describing the social behavior with especial regard for the relationship between parents and offspring. This was done principally by analyzing existing records of food intake by walruses in captivity at Marineland in California, and by conducting behavioral observations of two pairs of breeding adult walruses and their young in that same facility. Some information on cow/calf behavior of wild walruses also was obtained in the Chukchi Sea for comparison.

My primary objectives in conducting those studies were:

(1) To define the relationship of feeding rates to age, sex, season, and reproductive status of walruses.

(2) To describe the behavioral interactions between the calf and its parents.

In addition, I set out:

(3) To describe the visual and acoustical aspects of the courtship display of the male walrus.

(4) To describe the interactions between the male and the female in captivity, comparing them with the behaviors of walruses in the natural environment.

BACKGROUND

The walrus is a circumpolar arctic pinniped with two recognized subspecies: the Atlantic walrus, Odobenus rosmarus rosmarus (Linnaeus, 1758) and the Pacific walrus, O. r. divergens (Illiger, 1815). This study was of Pacific walruses under natural conditions in the Chukchi Sea, Alaska and in captivity at Marineland, Los Angeles, California.

Fay (1982) summarizes the annual cycle and basic life history attributes of Pacific walruses, which spend most of their life in association with the pack ice. They winter in ice-dominated areas of the Bering Sea, where they breed. In the spring as the ice melts and breaks up, the females, young, and relatively few of the adult males migrate northward into the Chukchi Sea. Along the way calving takes place, mainly in May. These walruses then spend the summer in the edge of the pack ice in the Chukchi Sea, while most of the adult males remain in the Bering Sea throughout the summer. In the summer, walruses undergo their annual molt, shedding and renewing their pelage. In the autumn when the ice forms southward, the females and young swim southward again to the Bering Sea, where they are rejoined by the males for the breeding season.

Most female walruses ovulate for the first time in their 6th or 7th year, but they do not reach full physical maturity until they are about 10 years old. Females between 8 and 15 years of age tend to calve bienially. Older and younger animals calve less frequently.

Males reach puberty between their 7th to 9th years. In their 10th to 14th years, they are capable of insemination but are considered to be subadults, because they do not reach their full physical development until they are about 15 years old. With full development, they become capable of competing with other mature males for access to mates and for aquatic territories in which to conduct their courtship displays during the breeding season.

The mating season for Pacific walruses is in the winter, mainly from January to February, while they are in the Bering Sea (Fay 1982). Adult males are fertile between November and April, whereas subadult males are fertile later in the breeding season, between December and May. Sexual interactions between males and females have been observed throughout the year, both under natural conditions and in captivity. During summer, subadult males engage in homosexual interactions with one another (Miller 1975b).

Pacific walruses gather to breed in two general areas within the pack ice (Fay 1982). These are in the north-central Bering Sea, between St. Lawrence Island and St. Matthew Island, and in the southeastern Bering Sea, in Kuskokwim Bay and Bristol Bay. The adult males and females congregate in those two areas from December to April. Females gather in herds with their young of previous years, and each such herd is attended by one or more adult males. Groups of subadult and juvenile males are found farther south, along the ice front (Popov et al. 1981; Fay 1982).

The walrus mating system has been described by Fay and Ray (1979:409) as resembling a "...lek system, in that the males engage in ritualized display in what could be regarded as small central territories. The subdominant bulls take peripheral positions and do not display, and male-female courtship and probably copulation, take place only or principally with the displaying bulls in the central area."

Aquatic mating displays have been reported for three species of ice-inhabiting pinnipeds in addition to the walrus. Male Weddell seals (Leptonychotes weddelli), bearded seals (Erignathus barbatus), and possibly harp seals (Pagophilus groenlandicus) trill and posture under water, apparently in courtship and territorial behavior during the breeding season (Ray 1967; Watkins and Schevill 1968; Ray et al. 1969; Schevill and Watkins 1971; Merdsoy et al. 1978; Burns and Frost 1979). The walrus also mates in an ice covered environment. Displaying male walruses associated with the herds of oestrous females station themselves 7 - 10 meters apart in the water in front of the ice floe where the females and young rest (Fay, Ray and Kibal'chich 1984). There they perform stereotyped behavioral displays, including both underwater and surface components.

Ray and Watkins (1975:525) described these courtship/territorial displays, as follows:

> "the male surfaces with a massive expulsion of air and rises out of the water to the level of the lower neck with the head erect and the tusks held horizontally as he inhales deeply. A sound pulse is heard at this time, after which the animal submerges just to the

> level of the back, floating horizontally in the water. The head is brought half out of the water two or three more times and each time a pulse is usually heard. Just before diving, a soft whistle may be heard. Surface pulses varied from 1 to 4 in number during the in-air component, the mode being 3. On all occasions, a final whistle signalled submergence for this individual. Other individuals apparently omitted the whistle. This animal invariably dived with the pharyngeal pouches fully inflated.
>
> The underwater pattern of display is much more complex. There are three basic sound patterns which are heard from a submerged male: in order (1) a double pulse followed by a bell sound (there may be several of these, or none); (2) a pulse series ending in a coda of seven sounds; (3) a final pulse series introduced by a triplet and ending with a strong final pulse which signals that the animal will soon surface".

The complete display lasts 2 - 3 minutes. Similiar displays have been observed in Atlantic walruses by Stirling et al. (1982), but the average duration of their displays was more than 9 minutes (N=10).

Ray and Watkins (1975:526) stated that walrus sexual displays appear to function "primarily in advertising the presence of a bull in breeding condition and perhaps the establishment of an underwater territory". Fay, Ray and Kibal'chich (1984) observed several agonistic encounters between male walruses. When one male left his area and approached another, the ensuing interactions involved rapid tusk strikes, diving and splashing, and lasted approximately 2 minutes. The aggressor then returned to his former "station", and both males continued their displays.

Male Weddell seals and male harp seals also have been observed to compete with each other to establish their dominance rank (Smith 1966;

Merdsoy et al. 1978). Those fights took place underwater beside the ice where one or more females were resting. Kooyman (1968:242) states that Weddell seals have a "...modified type of territoriality - modified in the sense that one seal does not defend the area to the complete exculsion of other seals, but actively defends it to the discouragement of other seals". Merdsoy et al. (1978) observed a male harp seal in a lead near a female who was on the ice. Whenever they approached that male underwater, he displayed aggressively. They also observed similar threat displays between male harp seals.

Sexual encounters between male and female walruses were observed during the winter by Fay, Ray and Kibal'chich (1984), but copulation was not seen, possibly because it took place underwater. Females left the herds resting on the ice and approached displaying males in the water. The pairs engaged in facial and bodily contact and dove together. After fewer than 3 minutes, the females left the males and returned to their herds on the ice.

Following mating in January and February, there is a four to five month period of delayed implantation (Fay 1982). The blastocyst does not implant in the uterus of the female walrus until June or July. Parturition takes place 10 to 11 months later, in the following May. At that time, the females are underway in their northward migration.

Fay (1982) suggested that, when a female walrus is ready to calve, she withdraws to an icefloe several meters to 1 kilometer from the herds of other females with young and gives birth. Fay's Eskimo

informants observed that females with newly born calves usually are found on "clean" floes, away from the placenta and bloody snow where the birth took place. For a day or two following birth, the female and calf often remain in isolation, then join other females with newborn calves, forming "nursery herds" of 20 to 50 animals (Burns 1970).

The bond between the female and her calf is stronger than in any other pinniped. The cow is exceedingly protective of her calf and may actively defend it from predators (Allen 1880; Collins 1940) and other walruses (Pederson 1962). This behavior probably has an effect on the entire walrus social system. In the event of the death of the mother, other walruses, even males, may respond to the distraught calls of the calf and take it away with them (Bel'kovich and Yablokov 1961). Adoption of a calf by a female other than its mother has been noted several times (Burns 1965; Eley 1978; Fay 1982).

The walrus calf nurses for at least 2 years, with the last 18 months involved in gradual weaning (Chapskii 1936; Loughrey 1959). This period of parental care is about 20 times longer than those of other pinnipeds inhabiting the same environment. For example, the ringed seal, Phoca hispida, and bearded seal, Erignathus barbatus, nurse their young for only 3 to 6 weeks (McLaren 1958; Burns 1967; Fay 1982). More than one year is required for the calf to quadruple its weight, whereas quadrupling of weight is accomplished in 3 to 6 weeks by the young of other arctic pinnipeds. The selective advantage of such a long parental bond is assumed to be increased survival and

recruitment, compensating for the low reproductive rate, which is about half that of other pinnipeds (Mansfield 1958a).

Partly because of that long period of parental care and the lesser need for rapid development of the calf, walrus milk is less rich than that of other pinnipeds. Fay (1982) estimated that the calf's daily net digestible energy intake is about the same as that for young domestic animals, and that the intake of solids after weaning is about 7% of total body weight (TBW) per day, decreasing to about 5% TBW/day in adulthood. Fay extrapolated from daily caloric intake of captive walruses that nonpregnant, non-lactating adult females would consume about 30% less food per day than adult males, and by analogy with domestic mammals (Brody 1945; Kleiber 1961) that the females' intake would double or triple during concurrent pregnancy and lactation.

METHODS

STUDY AREAS AND ANIMALS

Most of this study was conducted during five periods at Marineland in Los Angeles, California between 1980 and 1982. Additional observations were made from the icebreaker Polar Star, in the ice front of the Chukchi Sea in 1981.

I observed two pairs of adult walruses at Marineland. The elder pair was captured as newborn calves in May 1961 off St. Lawrence Island in the Bering Sea. Those calves arrived at Marineland when they were approximately two weeks old. The younger pair was captured during the summer of 1967 in the Chukchi Sea off Wrangell Island. Those calves arrived at Marineland in 1968, via the Moscow Zoo, when they were approximately one year old.

Each pair was housed separately in one half of a semi-circular enclosure (Figure 1). Each pair could hear and smell the other pair but not see them because of the separating wall between their pools. This wall rose 2 m above the water surface and sloped upwards so that it rose 3 m above the haulout platform. The water in each pool was 2.6 m deep, and the haulout platform was 1.5 m above the surface of the water. A ramp extended from the platform down to the surface of the water.

The elder pair first bred in the winter of their tenth year. Their first fetus, an 8 kg male, was aborted on 13 December 1971.

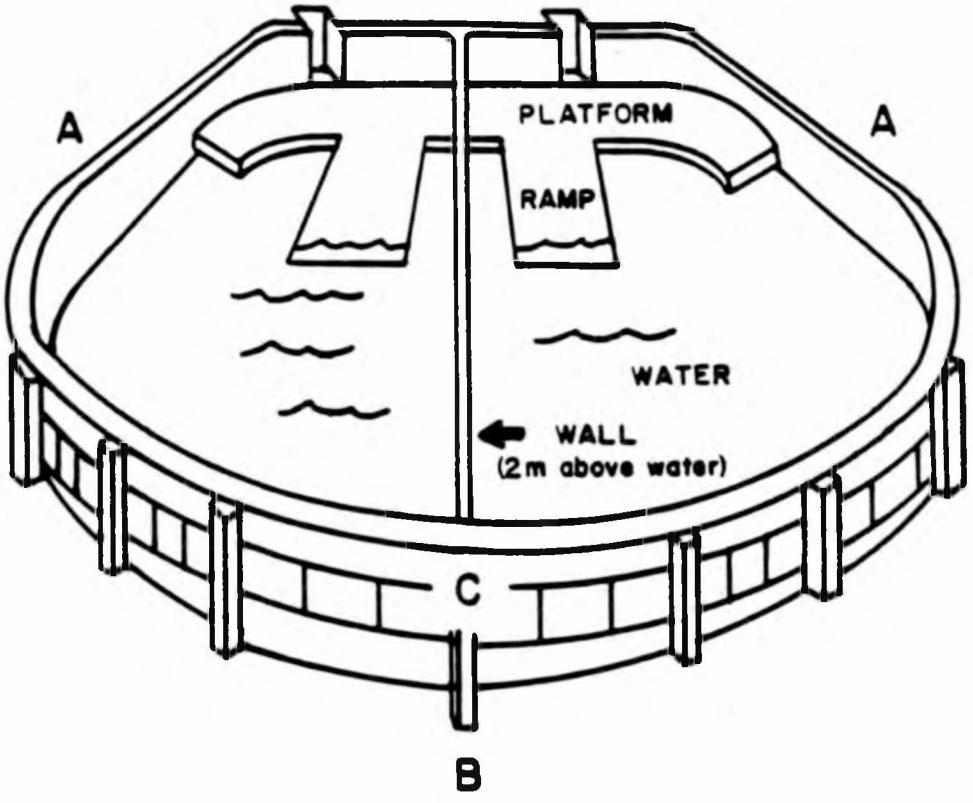


Figure 1. The enclosure at Marineland where the two pairs of adult walruses were housed. Behavioral observations were conducted from positions by the sides of the enclosure (A), in front of the underwater windows (B), and on the public observation platform (C).

When aborted, that fetus was an 8 kg male. The female of that pair was thought to have bred again in that winter, but a false pregnancy was suggested, because she failed to give birth in the spring of 1973. That pair bred again in the winter of 1974, and their second calf a female, was born on 20 May 1975. That calf died nearly a year later. Their third calf, a male, was born on 8 June 1978. That calf was separated from its mother about 1.5 years later and is still alive. Their latest calf, a female, was born on 29 May 1982. She died about one month later. I observed this calf during my study, up to eleven days before her death.

The younger pair of adults at Marineland also first bred in the winter of their tenth year. Their first calf, a female, was born on 7 July 1978 and was separated from her mother about 1.5 years later; she is still alive. Their second calf, a male, was born and died on 7 June 1981. I observed the birth of this calf during my study.

My observations of wild walruses were conducted during the second half of July 1981 in the eastern Chukchi Sea. Sixteen cow/calf pairs and 27 cow/juvenile pairs were observed in two general areas southwest of Barrow, Alaska (Figure 2). Those walruses were resting on ice floes in the ice front. Access to those walruses was gained by means of a small boat from the U.S. Coast Guard Icebreaker Polar Star.

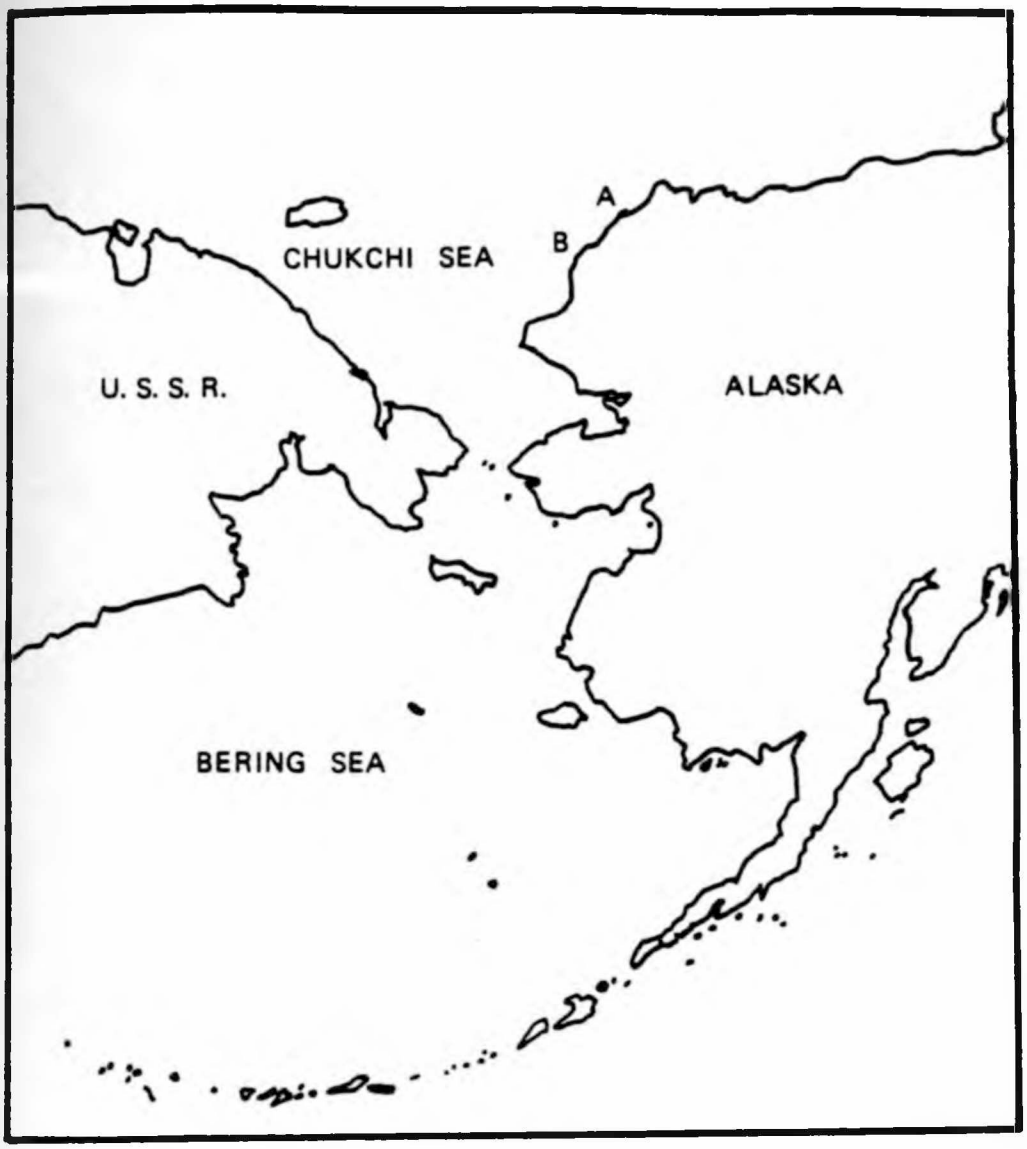


Figure 2. The locations where observations were made on wild walruses in the Chukchi Sea are indicated on this map at (A) and (B).

ENERGY INTAKE

The weight in pounds of each kind of food consumed by each walrus in Marineland was recorded daily by one of the attendants from 1974 to 1982. I converted those weights to gross energy values (kilocalories), based on the proximate composition of the foods from Geraci (1975) and the gross energy values from Pike and Brown (1975). With these values, daily gross energy intakes (kcal/da, kJ/da) were calculated for each walrus. Those rates first were compared graphically among the animals by plotting five day running averages for each animal in each year. Mean daily consumption rates then were compared among individuals, between sexes, among years for the same individuals and among barren, pregnant, and lactating females.

BREEDING BEHAVIOR

I observed the sexual behavior of the two pairs of captive walruses at Marineland during four study periods: 6-23 July 1980, 6-17 June 1981, 30 December 1981 - 6 January 1982, and 28 February - 13 March 1982. Both pairs were fully mature adults at those times, having bred and produced calves previously. The scheduling of observations differed among the five study periods. In July 1980, the periods of observation were about one hour long and were irregularly spaced (non-random). In June 1981, the periods of observation were two hours long and were randomly distributed through the daylight

hours. In December - January 1981-1982, the observation periods were about one hour long and were irregularly and non-randomly spaced. In February - March 1982, there were two to three observation periods of two hours each per day, which were randomly spaced during the daylight hours. Observation periods were scheduled to exclude the daily feeding sessions.

During the first three periods of study (July 1980 to January 1982), I observed the walruses from a central location on the public observation platform, three meters above the water level (Figure 1:C). I was able to observe both pairs concurrently from that location. At that time, I recorded my observations manually in a time-based narrative log. In the fourth study period, February - March 1982, I observed from the side of the exhibit, about one meter from the side of the pool (Figure 1:A). From that position only one pair could be observed at a time. Underwater behavior was observed from a central location, 2 m from the underwater viewing windows (Figure 1:B). From that position, I could observe both pairs concurrently. I spent approximately equal numbers of hours observing from above and below the surface. I recorded my observations at that time with a small hand-held tape recorder and later transcribed the data from those tapes. In each of the study periods, behaviors also were documented by photography.

Courtship displays by the males took place almost entirely in the "front" corner of each enclosure. I defined displays as starting when

the male arrived in that corner, and ending when he left it. The behaviors recorded during male courtship/territorial displays are defined as follows:

Bell - "Noises resembling those of church bells" (Brooks 1954:25), and "...bell-like tone which is made while the animal is submerged" (Fay 1960:369).

Bubble - The release of a stream of bubbles from the mouth while the head is underwater. No sound is heard (This Study).

Dive - "Submerge by diving beneath the water surface" (Ray and Watkins 1975). The animal submerges head first, and at least one of his hind flippers rises above the water surface (as compared with "Sink") (This Study).

Float - "The animal submerges just to the level of the back, floats horizontally in the water" with his back awash (Ray and Watkins 1975:525).

Pulses - "Made with the mouth shut and only movement of the upper lip" (Bel'kovich and Yablokov 1961:54). The skin under the lower jaw is drawn inwards, but the jaw does not move. Also the skin behind the top of the skull ripples with a movement down the neck. Pulses can occur in air and underwater (This Study).

Rest - A stationary underwater position. The animal lays his lower back on the floor of the tank with his shoulders against the dividing wall (This Study).

Sink - The animal passively submerges without raising his hind

flippers above the water surface (This Study).

Splash - While "Up" or "Floating" the animal slaps the water surface with one or both foreflippers and sometimes with the chin. The resulting spray rises approximately 1 to 2 meters into the air (This Study).

Splutter - The animal exhales through the lips, often with the mouth just below the surface of the water, so that the water bubbles around the face. A vocalization is heard which lasts about 2 seconds. It can be the beginning of a series of pulses. At other times, the animal exhales through the lips, when the mouth is above the surface of the water and makes this vocalization (This Study).

Surface - "Surfacing with a powerful exhalation of air" (Bel'kovich and Yablokov 1961:54), and the walrus "surfaces with a massive expulsion of air" (Ray and Watkins 1975:525). The spray may rise up to 1 meter above the water surface. This can also take place when the animal raises its head to breathe, while resting or floating (This Study).

Up - "Rises out of the water to the level of the lower neck with the head erect and the tusks held horizontally" (Ray and Watkins 1975:525). "The body angle was about 45° relative to the water surface and the face was out of the water (and not usually strongly directed up)" (Miller and Boness 1983:304).

Whine - Possibly a variation of the "Bell", without the "initial striking pulse" (Watkins and Ray pers. comm.). This has never been

recorded in the wild. As I observed it, it takes place underwater. The first part resembles a deep rumble, followed by a high-pitched whine, with a release of a stream of bubbles from pursed lips (This Study).

Whistle - During courtship displays, just before diving, male walruses emit a shrill clear sound. This whistle has been qualitatively described in several ways (Ray and Watkins 1975; Miller 1975b; Fay 1982). The lips are pursed and the mouth is open slightly, just above the water surface, while the male is "Up". The captive walruses that I observed whistled for approximately 1 - 2 seconds (This Study).

The data on the occurrence of courtship displays with respect to time of day and the frequency of displays were analyzed using the Chi-square test for independence. and the Mann-Whitney test (Zar 1974).

To examine the question of random versus stereotyped male display behaviors, I conducted a Markov Chain Analysis on the behaviors of each male displaying in his enclosure. Markov chains are sequences of behavioral states for which the transition from one state to another is governed by probability. Markov Chain Analysis assumes that the animal performs its next behavior solely on the basis of its most recent behaviors, and not on any of the preceding ones. In this work a chain of order one is specified; only the immediately preceding behavior is operative. More specifically, for the data here, the Markov chains are:

1. Finite: the number of steps are finite. This restric-

tion was imposed by the experimenter.

2. Irreducible: Every state can be reached from every other state, although not necessarily in one step.

3. Aperiodic: The interval before a return to a given state is not restricted to multiples of a fixed number of steps, for example, 2,4,6,...., other than unity.

It follows that the chains are:

4. Ergodic: The absolute probabilities of arriving at a given state converge, as the number of steps increases, to fixed values (Hiller and Lieberman 1967).

Essentially, this implies that a condition of equilibrium is eventually reached which is independent of the probability distribution of the starting states. An illustration of this technique is given in the Results section.

Within this framework it is possible to examine the reality of observed behavioral patterns. This was examined, in part, by raising the power of the one-step transition probability matrix to increasingly higher powers. When the matrix is raised to a power, the entries are multi-step probabilities. These indicate the probability of a behavior following another in 2 steps (when the matrix is squared), in 3 steps (when cubed) and in n steps (when the matrix is raised to the power of n). If "A" is a transition probability matrix whose $(i,j)^{th}$ element is the observed probability of changing from behavior "i" to behavior "j", then "A^n" is the n step matrix whose

$(i,j)^{th}$ element is the probability of changing from "i" to "j" in "n" steps.

As n increases, the rows become identical. Each entry in a row is then the steady-state probability of the process being in the state denoted by the pertinent column. This implies that the probability of being in a given state, after "n" steps, is independent of the initial state. The term "steady-state probability does not imply that the process settles down into one state. On the contrary, the process continues to make transitions from state to state" (Hiller and Lieberman 1967:361).

The power required to give such row convergence is a measure of the number of steps taken, from a randomly chosen start, to achieve a set of steady-state probabilities. A comparison of these powers gives the speed with which the animal, on starting its display performance, stabilizes its behavioral pattern.

Using the probabilities in the transition probabability matrix, all the possible cyclic permutations of five behaviors were defined and their empirical probabilities calculated. This was also done for cycles of three, four and five behaviors. The cycles that were most likely to occur were the highest of these empirical probabilities in each group (3,4 or 5 behaviors). The probabilities of the most frequent five-behavior sequence for each male were compared during and outside the breeding season. The equations used and the calculations are shown in Appendices G-J.

INTERACTIONS

Interactions were considered to occur when the male and female walrus were within one meter of each other for more than 10 seconds. The interaction was considered to follow a courtship display if it took place within one minute of the male leaving the display corner, or if the female joined the male while he was displaying. The criterion of "one minute" was arbitrary, but was based on the behavior of the walruses in this study. After a male left the display corner he either initiated an interaction with the female or swam around the enclosure. My observations suggested that if an interaction followed a display by less than one minute it was affected by the occurrence of that display, but if it followed the display by more than one minute, the display had no effect on it. Behaviors recorded during interactions were defined as follows:

Bark - "A short loud explosive cry" (Gove 1976:177).

Chase - One animal follows the other "rapidly and intently ... as if to ... overtake it" (Gove 1976:379; Salter 1978).

Expirations - "These range from broad-band snorts and guttural, pulsed coughs to tonal Roars" "given by threatening walruses before and after striking or feinting, usually while the head is held high in tusk-threat" (Miller and Boness 1983:309).

Face Away - "Respond to a close-up threat" by "leaning away" and orienting the head away from the aggressor. "The action often seems

to be one of simple avoidance" (Miller 1975b:594).

Female Mount - The female "mounted the male's back in what appeared to be a 'copulatory' position with the male and female roles reversed" (Fay, Ray and Kibal'chich 1984:15).

Flipper - "Walruses respond to numerous disturbances by flippering the other interactant with fore(usually) or hind flippers or both" and "flippering is used strategically by submissive and aggressive animals" (Miller 1975b:594).

Groan - "A deep usually inarticulate and involuntary often strangled sound" (Gove 1976:1001). "A quiet bark" (Bel'kovich and Yablokov 1961:54).

Kinesic Visual Tusk Threat - "The head is shaken laterally, rapidly and repeatedly, as though to contact the recipient's tusks. The other form is a rapid movement downward in the direction of the recipient. as though to strike his face or throat" (Miller 1975b:592; Miller 1975a).

Lean Protectively Against - "Subordinate walruses can often protect themselves from being struck by leaning against the side and upper back or dorsal neck of a threatening superior" (Miller 1975b:594).

Male Mount - The male mounted the female's back in a copulatory position (This Study).

Naso-Nasal Greeting - Touching, snout-to-snout, with "Slight tilting of head downward, thereby bringing the dorsally positioned

nostrils in proximity...the vibrissae moved slowly but obviously throughout the engagement" (Miller 1975a:271).

One-Way Olfactory/Tactual Investigations - Exploring, using the mystacial pad to investigate another walrus or an object (Miller 1975b).

Static Visual Tusk Threat - "The head of the sender is raised and thrown back so that the tusks are held roughly horizontal and point directly toward the recipient" (Miller 1975b:592).

Swim - "To move or propel oneself progressively in water by ... movements of the flippers" (Gove 1976:2312).

Tusk Strike - "With the tusks, is usually performed with a downward motion, so that the recipient is usually struck with the tips of the tusks" (Miller 1975b:594).

Underwater Approaches - One animal advances to within 1 meter of the other while swimming (This Study).

Wrestle - Swimming erratically, pushing and pulling each other with the flippers (Salter 1978).

Even though three of the four adult walruses at Marineland did not have tusks, their head movements associated with their threat behaviors (tusk strikes, static and kinesic tusk threats) were the same as those described by Miller (1975b) for wild males with tusks.

The interaction data were examined by means of the Chi-square test, the Mann-Whitney test, and the Binomial test.

COW/CALF BEHAVIOR

I observed the birth of a walrus calf to the younger pair of adult walruses at Marineland on 7 June 1981. I began my observations of the female in labor at 0500h on that day and observed almost continuously until 1607h, when the calf died. Observations were recorded in a narrative log and with photographs.

I also observed the elder pair of walruses at Marineland and their newborn female calf for 94 hours from 29 May to 14 June 1982. During that study period I observed from the side of the exhibit about 1 meter from the side of the pool (Figure 1:A). Starting at 1025h on 29 May, about 9 1/2 hours after the birth of the calf, I observed the three animals intermittently for half-hour periods, one hour apart, until 0930h on 30 May. I observed the animals in three 2-hour periods per day, with randomly scheduled intervals of 30 minutes and 1 hour between them, each day. Each day's observations also were randomly scheduled to take place in either the first half (0600h - 1300h) or the second half (1300h - 2000h) of the daylight hours. If a suckling bout was in progress at the end of a scheduled 2-hour period, observation was continued until the bout was finished.

On five days between 20 and 28 July 1981, I observed wild cow/calf and cow/juvenile (1 - 3 years) pairs of walruses in the Chukchi Sea. The animals were resting on ice floes and were observed from a small boat and from neighboring floes. The observations took place between 0945h and 2025h. Durations of observations of individual

pairs ranged from 24 seconds to 2 hours and 25 minutes.

Behaviors of both the Marineland cow/calf pair and the wild pairs were recorded in a time-based narrative log, using a small hand-held tape recorder, in addition to manually-recorded notes and photographic ducumentation. The behaviors of both the Marineland and Chukchi animals are defined as follows:

Alert - "A state of readiness", "careful zealous watchfulness and promptness to counter threats and dangers and to cope with emergencies" (Gove 1976:51). The walruses "spontaneously interrupted their sleep periods to become noticeably alert (i.e., to raise their heads)" (Salter 1978:55).

Approach - One member of the cow/calf pair moves to within one calf length (about 1 meter) of the other (This Study).

Bellow - "A loud deep hollow prolonged sound" (Gove 1976:201). "A loud, repeated tonal call given by dependent young under numerous circumstances, particularly when troubled... At high intensity, Bellowing is rapidly and rhythymically repeated. At low intensity, Bellows are emitted more slowly and irregularly, are softer, and are often longer." (Miller and Boness 1983:308).

Expose - The female rolls onto her side exposing her abdominal mammae. This is the suckling position (This Study).

Leave - One member of the cow/calf pair withdraws to more than one calf length from the other (This Study).

Pup Contact Call - A loud hoarse vocal utterance used "by females

toward their offspring" (Miller and Boness 1983:310). This has been called a "soft tonal call" (Miller and Boness 1983:310). In this study it was not always a soft call; often it was very loud.

Push - An animal physically maneuvers or attempts to maneuver another with its flipper, shoulder or head (This Study).

Recumbent and Apparently Sleeping - The animals are resting on the substrate with no noticeable movement (Salter 1978).

Roar - "A full loud reverberating sound" (Gove 1976:1963). This is a threat vocalization given by female walruses in defense of their offspring (Bel'kovich and Yablokov 1961).

Suckle - An animal takes in nourishment by nursing from a lactating female "on land, in the water and on ice pans" (Salter 1978:54).

In this study, I recorded the orientation of the calf's body relative to the mother's body (reverse parallel, right angle (Salter 1978) or parallel), in addition to the duration of each suckling bout (Figure 3). The durations of breaks of more than 10 seconds between individual suckles were recorded; shorter breaks were not recorded. To address the question of how protective the cow is of the calf. I noted separations (when the pair was more than one calf length apart) and reunions. In addition, I noted who used vocalizations during a separation, as well as who left and who approached (rejoined).

Activity patterns for the calf were analyzed in relation to time of day. Inactivity was defined as lying still for ten or more seconds

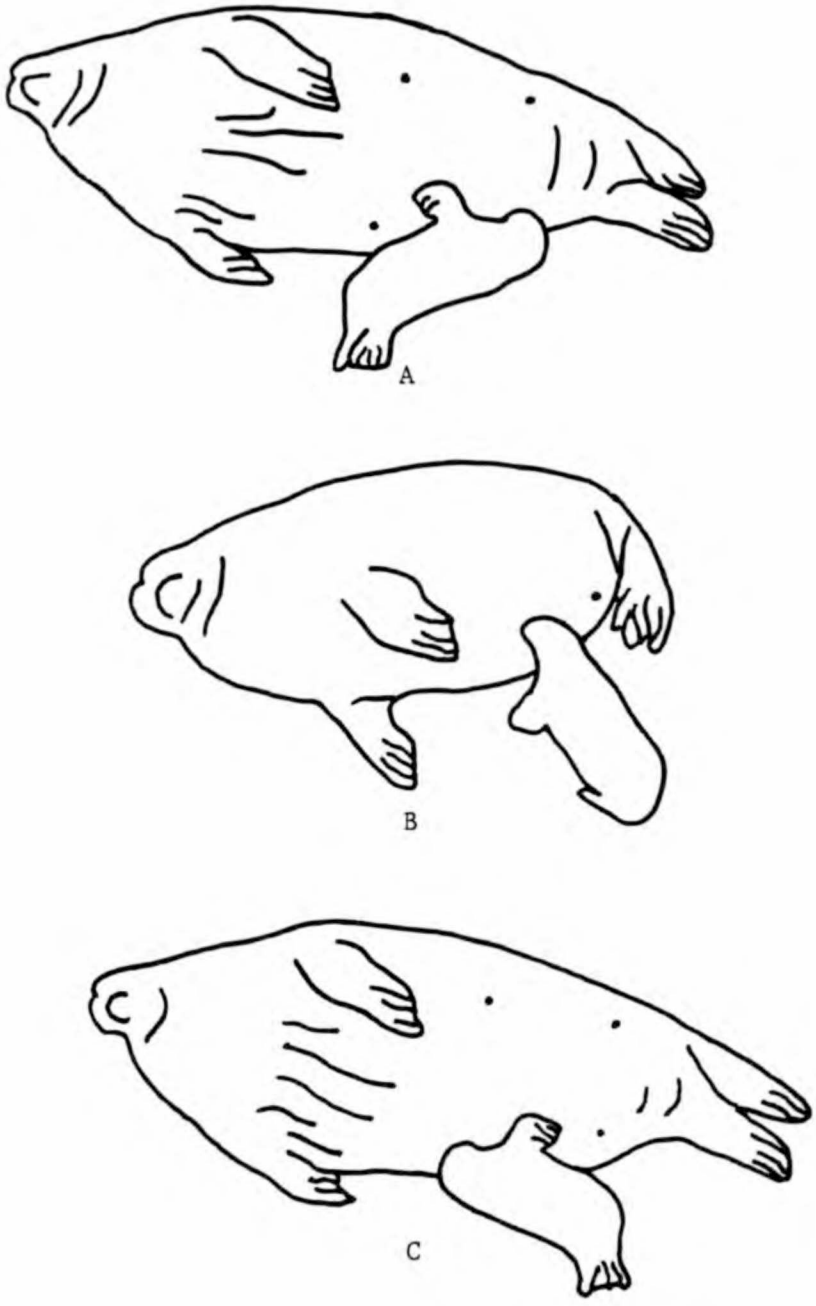


Figure 3. The orientation of the calf's body relative to the mother's body during suckling bouts (Reverse Parallel, A; Right Angle, B; and Parallel, C).

in which no more than one passive behavior occurred.

The behavioral data collected during observations of the cow/calf pair at Marineland, and the pairs in the wild, were examined by means of the Chi-square test, the Mann-Whitney test, the Binomial test, and the Wilcoxon Paired Sample test (Zar 1974; Conover 1980).

RESULTS

ENERGY INTAKE

The Marineland walruses consumed energy annually at mean rates ranging from 25,119 to 70,307 kcal/day (Figure 4 and Appendix I). The daily mean intakes for both the males and the females increased with age up to about 7 years. At that point, the consumption rate for females tended to level off, while that for males rose again before leveling off at about 16 years. Pregnant and lactating females consumed more energy than did nonpregnant and nonlactating females, but they mostly ate less than did the adult males.

To estimate the consumption rate in relation to body weight, I assumed that the total body weight (TBW) for a given age was about the same as the mean TBW for wild walruses. Fay's (1982 fig. 21) comparative data indicated that the weights of wild and captive animals were comparable. On that basis, I calculated that the captive walruses consumed from 238 to 472 kcal/$kg^{3/4}$ TBW per day. That is, their intakes in relation to "metabolic body size" (Kleiber 1961:209) were similar to those of domestic animals. Those consumption rates were highest in the young growing animals and lowest in the adults; they tended to decrease continuously with increasing body size and age (Figure 5).

The female walruses consumed more energy during pregnancy than

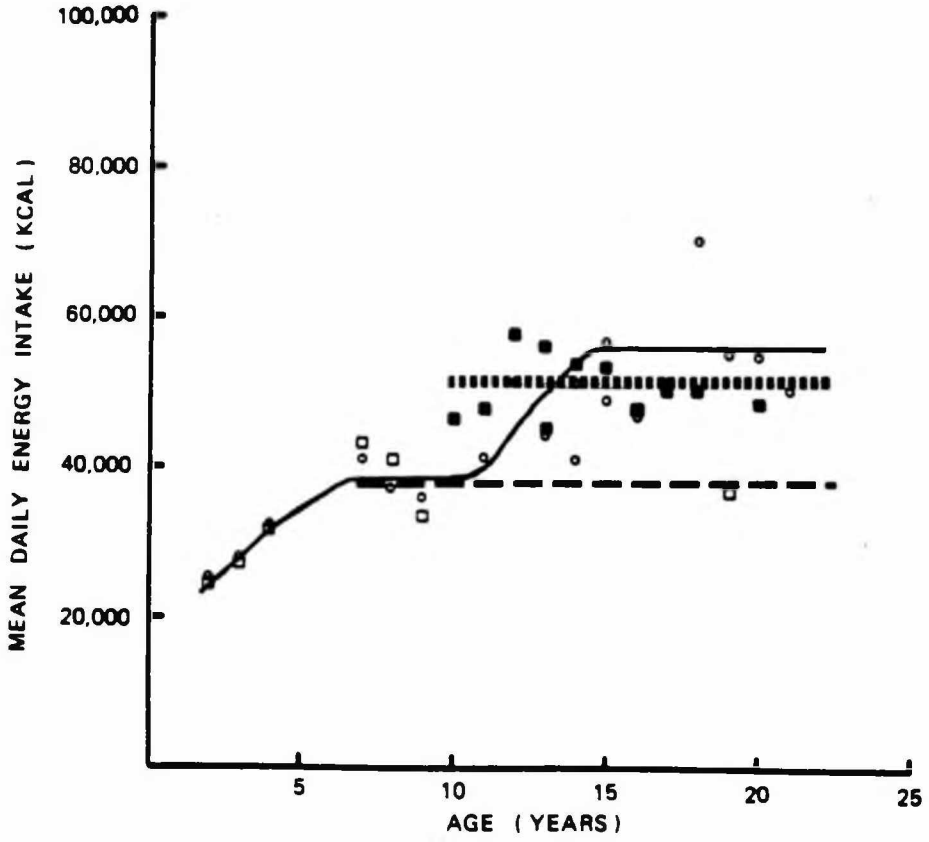


Figure 4. Mean daily energy intake in relation to age of male (circles) and female (squares) walruses at Marineland. Each point for males and for non-pregnant and nonlactating females is the daily mean for one animal for one year. For pregnant and lactating females (solid squares), each point is for the calendar year in which they were pregnant and/or lactating. The data are shown in Appendix I. The curves for the males (———), females (- - -), and pregnant and/or lactating females (▮▮▮▮▮▮▮) were estimated visually.

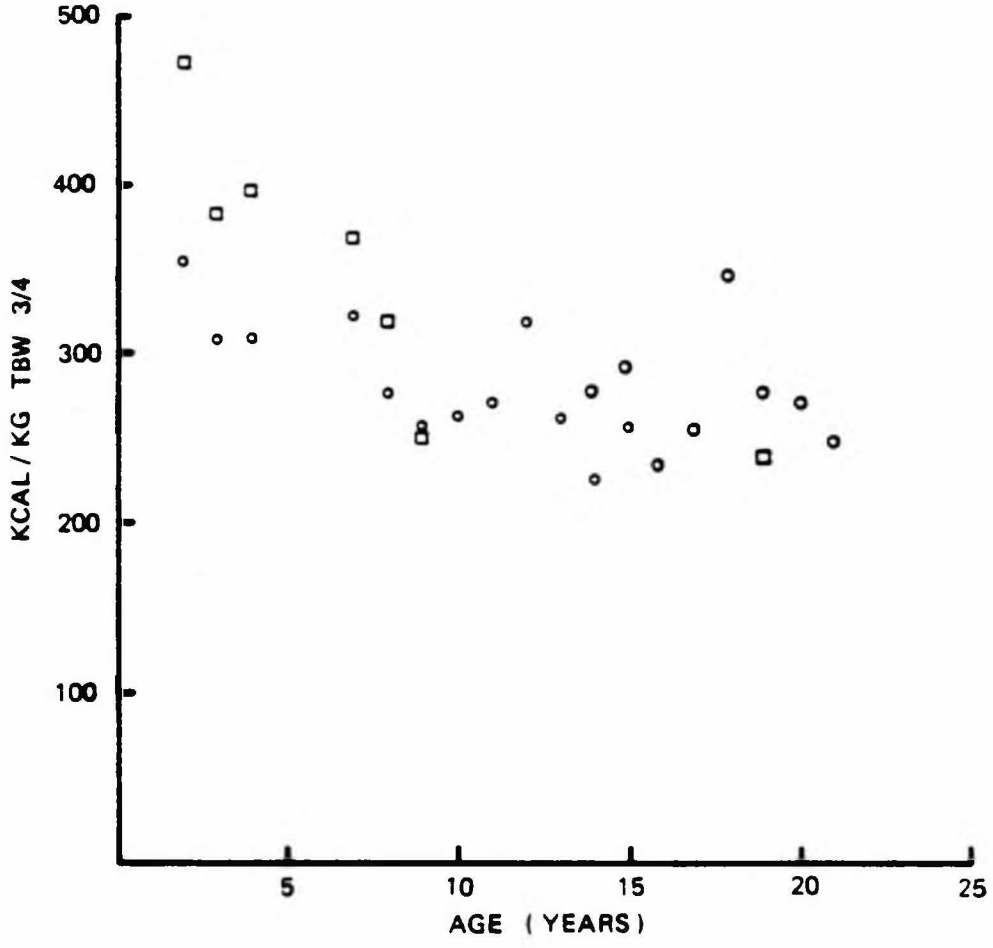


Figure 5. Mean kilocalories consumed per kilogram total body weight raised to the 3/4 power, per day, in relation to age for the male (circles) and female (squares) walruses at Marineland. Pregnant and/or lactating females have been excluded.

when not pregnant. Following fertilization, their daily consumpion of energy tended to increase steadily, usually reaching its maximum during the following November or December (Figure 6 and Appendix II). Feeding rates usually decreased over the next three months, then fell abruptly to zero for several days about the time of birth. The overall mean daily consumption of energy in each of the five pregnancies for which I had data, from the first increase after fertilization until the decline at calving, ranged from 49,250 - 57,963 kcal/day or 318 - 375 kcal/$kg^{3/4}$ TBW (Table 1). This is approximately 40 - 50% higher than the means for the same females of comparable age when nonpregnant and nonlactating, which ranged from 33,685 - 36,834 kcal/day or 238 - 248 kcal/$kg^{3/4}$ TBW (Appendix I). The mean daily intake at the maximum in November and December during those five pregnancies ranged from 52,522 - 69,260 kcal/day or 340 - 448 kcal/$kg^{3/4}$ TBW (Table 2).

The female walruses also consumed more energy while lactating than they did when not pregnant or lactating (Table 3). The mean energy consumption values for the first year of lactation for three lactation periods ranged from 50,477 - 55,498 kcal/day or 336 - 359 kcal/$kg^{3/4}$ TBW. Those values are approximately 50% greater than the energy consumption rate for the same females at comparable age when nonpregnant and nonlactating. That energy consumption decreased immediately when the cow and calf were separated and thereafter remained at the nonpregnant, nonlactating level for females (Figure 7).

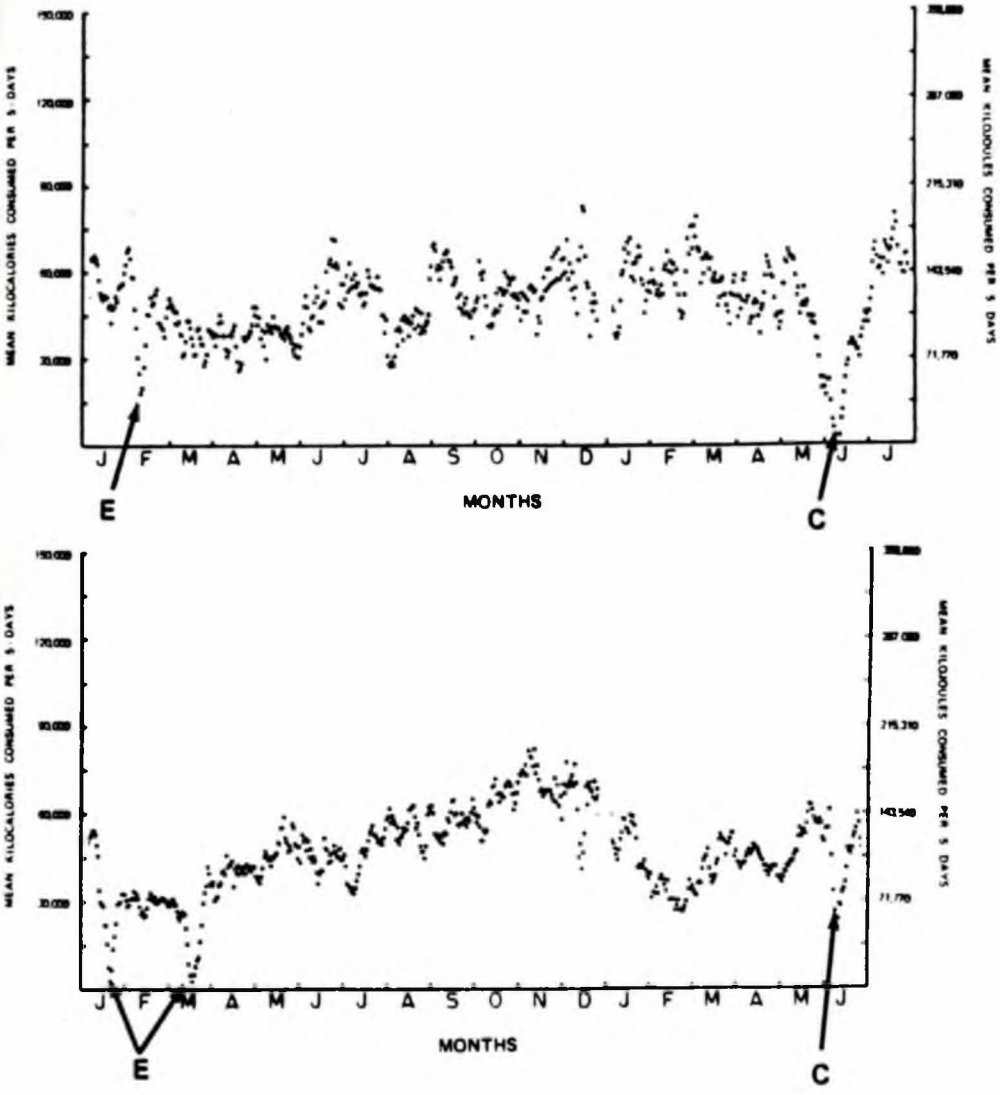


Figure 6. Five point running averages of daily energy consumption during one pregnancy of the older (upper) and younger (lower) female walruses at Marineland (E = Estrus, C = Calving). (For additional records, see Appendix II).

Table 1. Mean daily consumption of energy by female walruses at Marineland during five pregancies.

Female	Age (yrs.)	Pregnancy	Mean daily intake[1]	
			kcal	$kcal/kg^{3/4}TBW$
Younger	10	1st	50,787	354
Younger	13	2nd	49,250	318
Older	13	2nd	57.963	375
Older	16	3rd	50,873	329
Older	20	4th	52,385	339

[1] The mean daily consumption of energy during pregnancy was calculated from the time of increase following fertilization to the time of decline at calving.

Table 2. Mean daily consumption of energy during the period of maximal caloric intake (November - December) in five pregnancies of female walruses at Marineland.

Female	Age (yrs.)	Pregnancy	Mean daily intake	
			kcal	$kcal/kg^{3/4}_{TBW}$
Younger	10	1st	61,423	429
Younger	13	2nd	63,552	411
Older	13	2nd	69,260	448
Older	16	3rd	55,519	359
Older	20	4th	52,522	340

Table 3. Mean daily consumption of energy during one year of lactation for female walruses at Marineland.

Female	Age (yrs.)	Pregnancy	Mean daily intake	
			kcal	kcal/kg$^{3/4}$TBW
Younger	11	1st	50,477	336
Older	14	2nd	54,764	354
Older	17	3rd	55,498	359

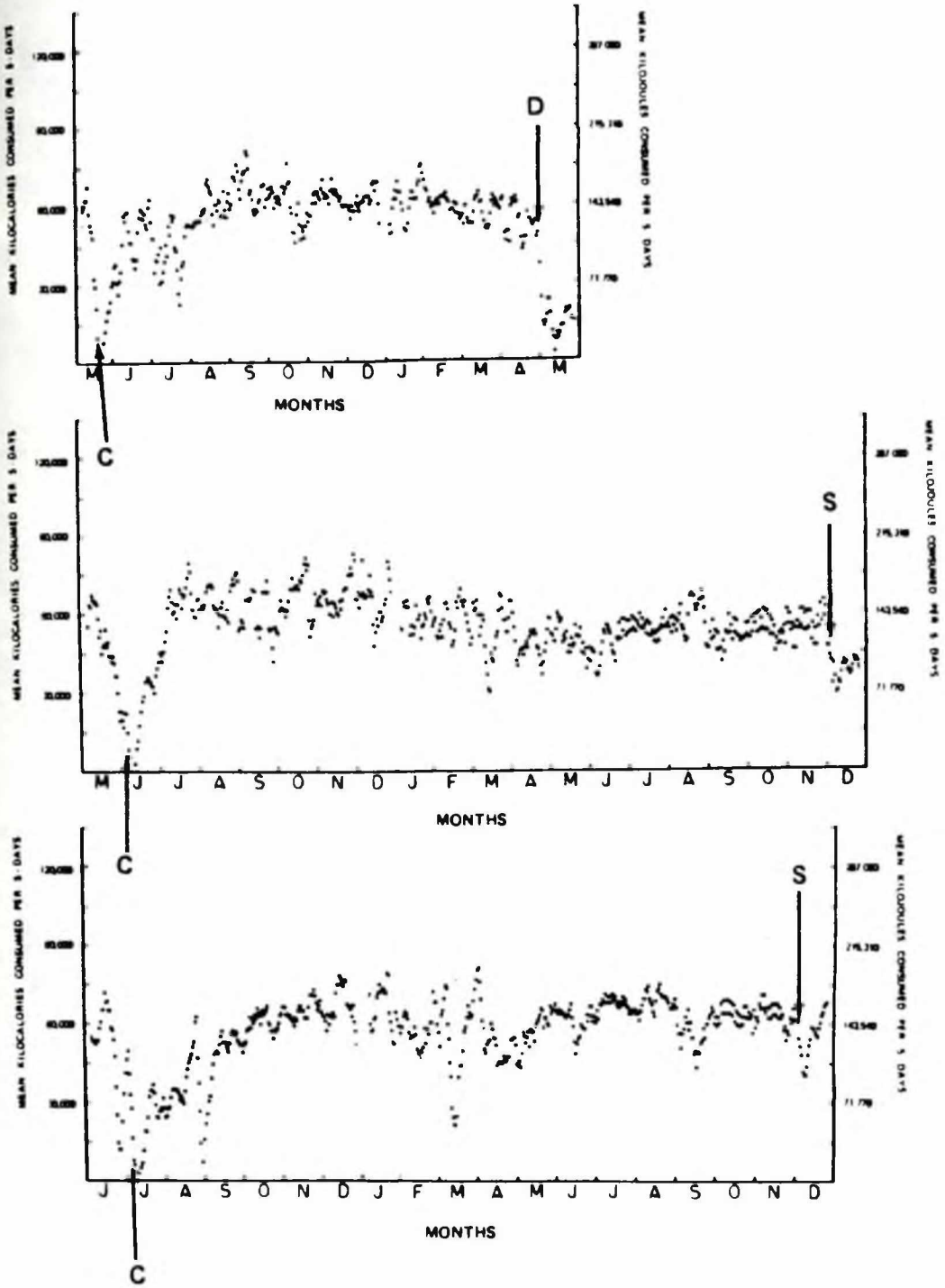


Figure 7. Five point running averages of daily energy consumption during lactation for the older (upper two figures) and the younger (lower figure) female walruses at Marineland (C = Calving, S = Separation, D = Death).

During the breeding season, the adult males tended to eat much less than they did at other times of the year (Figure 8 and Appendix III). On some days, they ate nothing. They began this decreased intake as subadults, and showed it most markedly by their 10th year, in which they also first bred successfully. After that time, the duration and depth of the low intake periods increased each year, with increasing age of the animal. To counterbalance their fasting in the breeding season, they increased their mean daily consumption rate outside the breeding season (Figure 9). That consumption rate increased with increasing age and apparently had not begun to level off, even by the time the elder male was 20 years old. Since the overall mean daily intake per year leveled off at approximately 16 years, the continually increasing intake with age outside the breeding season indicates increasing depth and duration of the fast during the breeding season.

Each winter when the female walruses were not pregnant or lactating, they stopped eating for a day to a week, usually in January or February (occasionally in March). Then, they resumed their consumption at the previous level (see Figure 5 and Appendix II). I believe that those days of zero intake were at the time of ovulation. This was suggested further by the behavior of the males, who also fasted on those days (Figure 10). In several instances, (see Figure 6) the females about 4 to 6 weeks after birth also fasted for a few days, at the time of the postpartum estrus (Fay 1982).

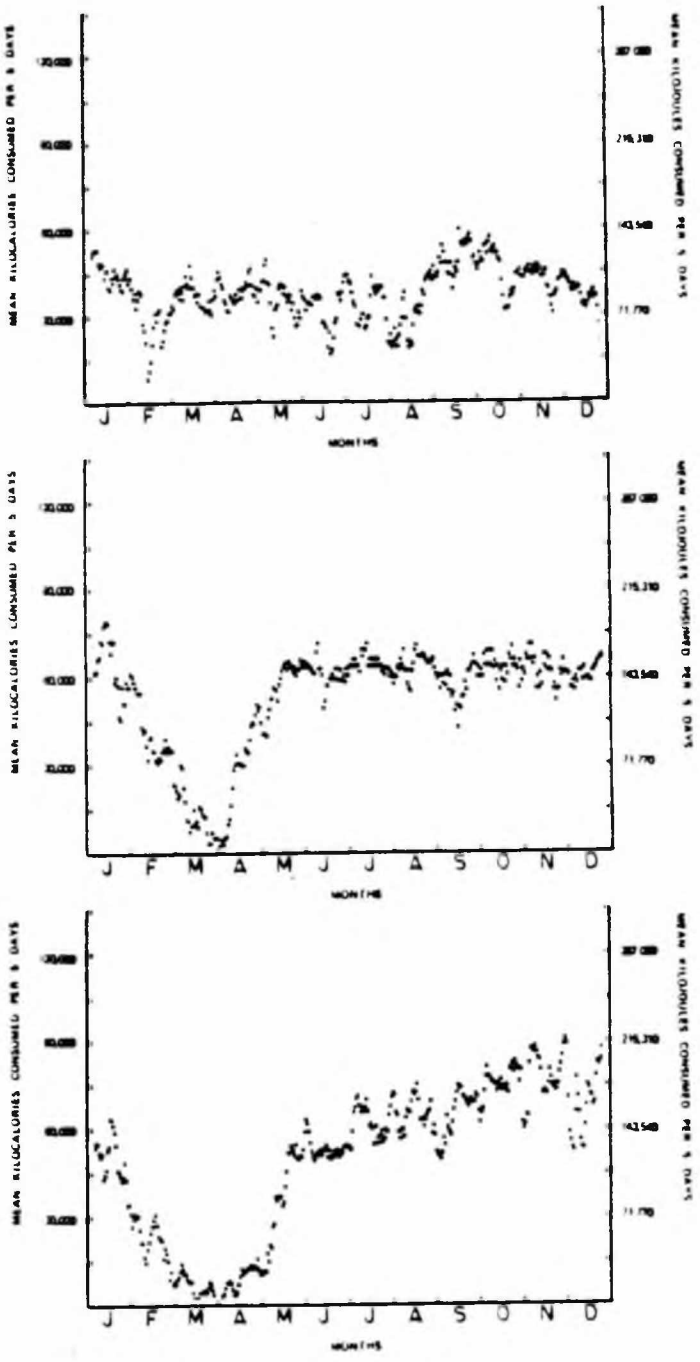


Figure 8. Five point running averages of daily energy consumption for one male walrus at Marineland at 8, 12, and 15 years of age. (For additional records, see Appendix III).

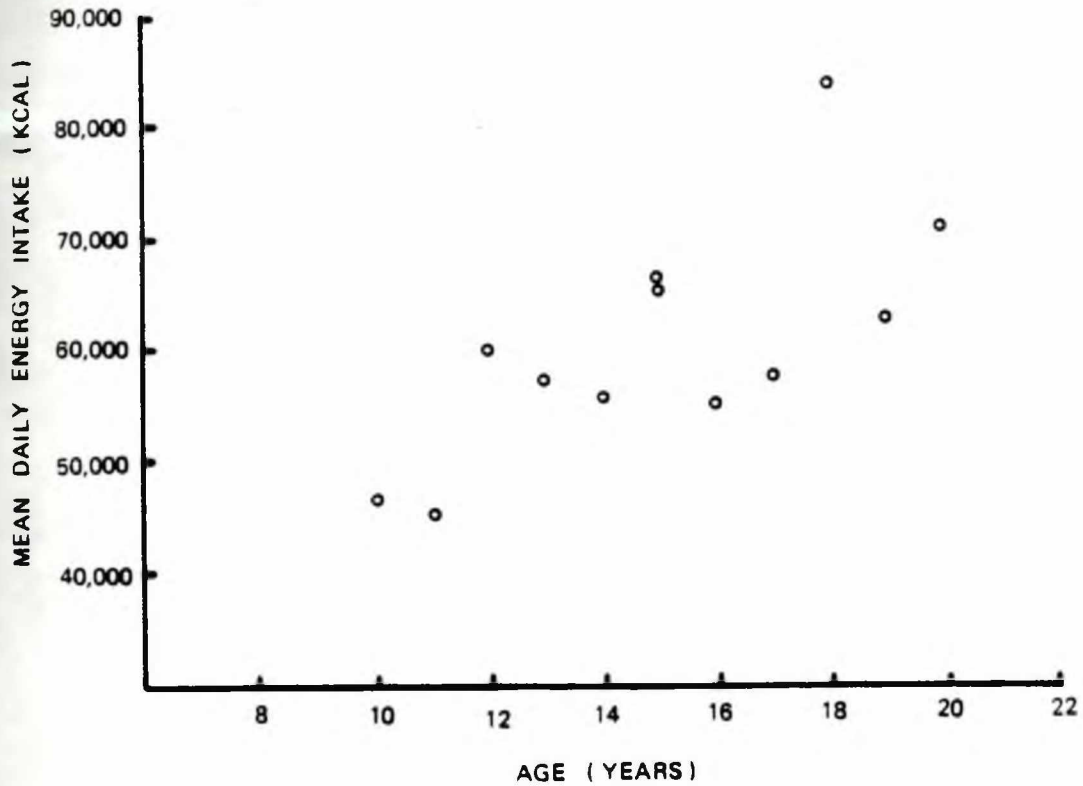


Figure 9. Mean daily energy consumption for two male walruses at Marineland outside the breeding season.

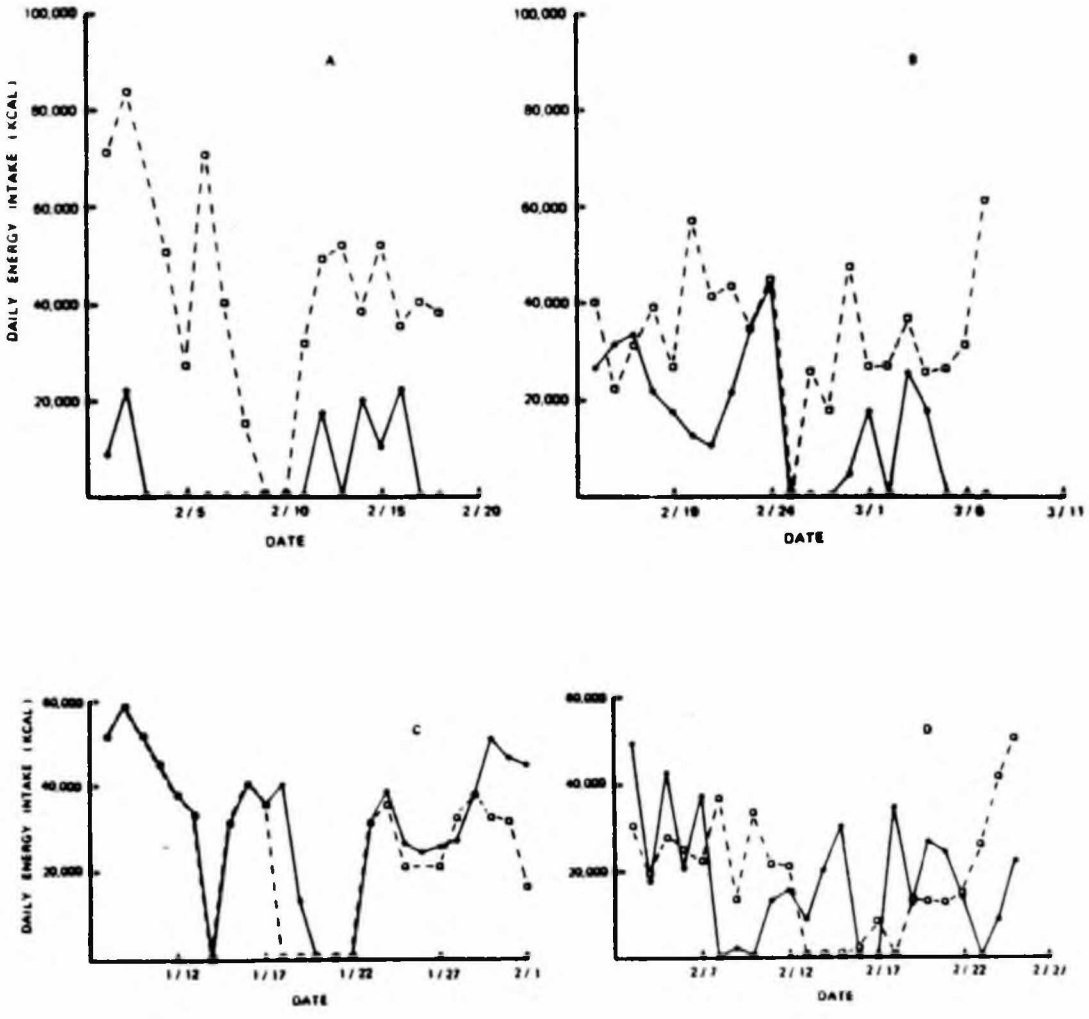


Figure 10. Daily energy consumption by the older (A, 1977) and the younger (B, 1977; C, 1980; D, 1980) pairs of walruses at Marineland, at the time when ovulation was believed to have taken place (Males (———) and Females (— — —)).

BREEDING BEHAVIOR

Each pair of walruses at Marineland was isolated from the other by the separating wall between their enclosures. For that reason. the adult males were unable to see each other or to compete for space or for mates, but they were accoustically and probably olfactorily aware of each other's presence and activities. Their awareness of each other was indicated by repetitious aspects of their behavior. First, they displayed on opposite sides of the separating wall, always in adjacent front corners of their respective pools (Figure 1C). Second, when one male began to display, the other often approached his respective display site within a few seconds (Median=12 sec, Range=1-738 sec, N=162) and began to display. Third, when both males were displaying, they tended to perform alternately; while one conducted the active, swift-moving parts of its display, the other male floated or rested; then the second became active while the first rested, etc.

Both males displayed more frequently during the breeding season than at other times (10.1/hr. vs. 3.1 displays/hr., Z test=21.5874, $p<0.001$). The displays of both males also were shorter but involved more behaviors during the breeding season than at other times (Tables 4,5).

During the breeding season, both males spent more of their time displaying during the middle of the day, than in the morning or the evening (Figure 11). During the rest of the year, the elder male

Table 4. Mean durations of courtship displays by two adult male walruses during the breeding season vs. outside the breeding season at Marineland.

Male	Displays during breeding season		Displays outside breeding season		Mann-Whitney	
	N	Duration (Sec.)	N	Duration (Sec.)	U	p
Youngest	540	153	266	231	55,962	<0.001
Oldest	465	94	184	365	15,714	<0.001

Table 5. Mean numbers of behaviors per courtship display by two male walruses during the breeding season vs. outside the breeding season at Marineland.

	Displays during breeding season		Displays outside breeding season		Mann-Whitney	
Male	N	No. behaviors	N	No. behaviors	U	p
Youngest	545	17	265	9	90,195	<0.001
Oldest	464	10	183	9	48,501	<0.001

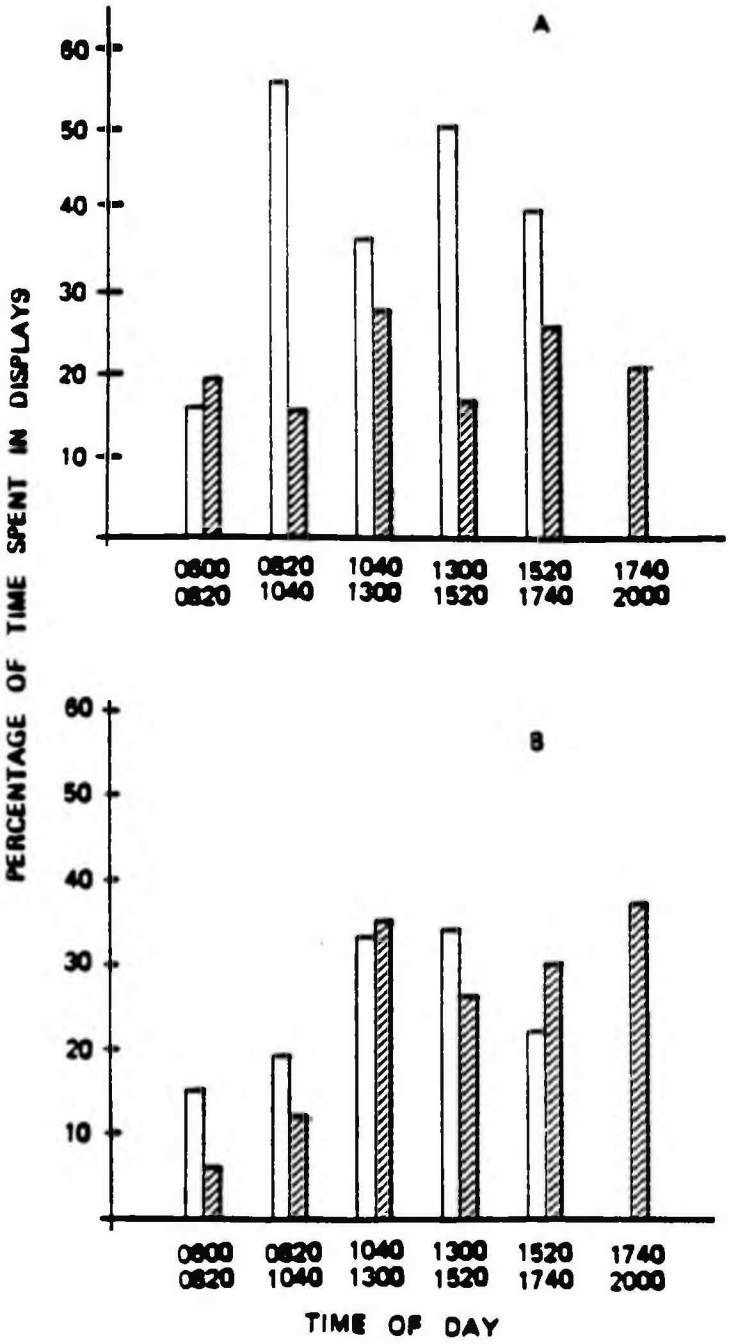


Figure 11. Percentage of time spent by the younger (A) and older (B) male walruses in displays during the breeding season (open bars) and outside the breeding season (cross-hatched bars) in relation to the time of day.

displayed mainly during the second half of the day, whereas the younger male displayed at about equal rates through the day.

To define the sequences of behaviors that were performed during the males' courtship displays, a Markov Chain Analysis was done on the display behaviors. In that analysis the first step was the development of a transition frequency matrix, which showed the number of times that each of the display behaviors followed any other behavior. An example is shown in Table 6 and Appendix IV. That matrix then was transformed into an empirical transition probability matrix which showed the probabilities of changing from one behavior to another (Table 7 and Appendix V).

The transition probability matrix was raised to increasing powers of n. When a matrix was raised to the third power, for example, the probabilities were those of progressing from one behavior to another in three steps; when raised to the fourth power, the matrix showed the probabilities of progressing in four steps, and so on. At high powers of n, the rows of a given matrix became identical (Table 8 and Appendix VI). As noted earlier, each entry in a row is not the observed proportion of the various behaviors; rather. it is the long run probability of the process being in the state denoted by the pertinent column. The powers to which the matrices had to be raised to make the rows equal, to within 0.0001, are shown in Table 9. This table shows that after a random start, stable state probabilities are reached in fewer steps outside the breeding season (fast converging matrix) than

Table 6. The transition frequency matrix from first to second behaviors[1] for the older male walrus at Marineland, during observations from above the water in the breeding season. (For additional transition frequency matrices, see Appendix IV).

		SECOND BEHAVIOR										
		1	2	3	4	5	6	7	8	9	10	11
FIRST BEHAVIOR	1	0	81	316	1	8	0	0	0	0	0	0
	2	3	0	1	216	4	17	1	1	2	8	5
	3	0	74	0	10	142	0	2	1	1	0	2
	4	264	5	10	0	1	0	0	0	0	1	0
	5	4	29	10	50	0	9	0	5	1	2	1
	6	5	6	8	1	3	0	0	0	1	0	0
	7	0	0	0	2	1	0	0	0	0	1	0
	8	0	0	0	0	2	0	0	0	0	2	4
	9	0	2	1	0	1	0	0	0	0	0	0
	10	1	0	0	3	1	0	1	0	0	0	2
	11	0	0	0	0	0	0	0	2	0	3	0

[1] (1=surface, 2=up, 3=rest, 4=dive, 5=float, 6=sink, 7=splash, 8=whistle, 9=swim around, 10=pulses in the air, 11=splutter)

Table 7. The transition probability matrix from first to second behaviors[1] for the older male walrus at Marineland, during observations from above water in the breeding season. (For additional transition probability matrices, see Appendix V).

		SECOND BEHAVIOR									
		1	2	3	4	5	6	7	8	9	10	11
FIRST BEHAVIOR	1	0.0000	0.1995	0.7783	0.0025	0.0197	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
	2	0.0116	0.0000	0.0039	0.8372	0.0155	0.0659	0.0030	0.0030	0.0078	0.0310	0.0194
	3	0.0000	0.3190	0.0000	0.0431	0.6121	0.0000	0.0086	0.0043	0.0043	0.0000	0.0086
	4	0.9393	0.0178	0.0358	0.0000	0.0034	0.0000	0.0000	0.0000	0.0000	0.0036	0.0000
	5	0.0340	0.2613	0.0901	0.4585	0.0000	0.0811	0.0000	0.0450	0.0090	0.0180	0.0090
	6	0.2083	0.2500	0.3333	0.0417	0.1250	0.0000	0.0000	0.0000	0.0417	0.0000	0.0000
	7	0.0000	0.0000	0.0000	0.5000	0.2500	0.0000	0.0000	0.0000	0.0000	0.2500	0.0000
	8	0.0000	0.0000	0.0000	0.0000	0.2500	0.0000	0.0000	0.0000	0.0000	0.2500	0.5000
	9	0.0000	0.5000	0.2500	0.0000	0.2500	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
	10	0.1250	0.0000	0.0000	0.3750	0.1250	0.0000	0.1250	0.0000	0.0000	0.0000	0.2500
	11	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.4000	0.0000	0.6000	0.0000

[1] (1=surface, 2=up, 3=rest, 4=dive, 5=float, 6=sink, 7=splash, 8=whistle, 9=swim around, 10=pulses in the air, 11=splutter)

Table 8. Example of the long run steady-state matrix for the behaviors[1] of the older male walrus at Marineland during observations made from above the water during the breeding season. (For additional long run-steady-state matrices, see Appendix VI).

FIRST BEHAVIOR	SECOND BEHAVIOR										
	1	2	3	4	5	6	7	8	9	10	11
1	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200
2	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200
3	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200
4	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200
5	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200
6	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200
7	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200
8	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200
9	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200
10	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200
11	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0054	0.0157	0.0041	0.0252	0.0200

[1] (1=surface, 2=up, 3=rest, 4=dive, 5=float, 6=sink, 7=splash, 8=whistle, 9=swim around, 10=pulses in the air, 11=splutter)

Table 9. The powers (n) to which the one-step transition probability matrices had to be raised, until the rows became equal (to within four decimal places).

Male	During the breeding season	Outside the breeding season
Oldest	$34 < n \leq 64$	$9 < n \leq 16$
Youngest	$16 < n \leq 17$	$9 < n \leq 16$

during the breeding season (slow converging matrix).

Using the probabilities from the transition probability matrix from surface observations that were made during the breeding season, I calculated the empirical probabilties of the permutations of 3-, 4-, and 5-behavior cycles. Several distinct behavioral sequences during the breeding season had higher empirical probabilities than any behavioral sequence outside the breeding season. During the breeding season, the older male performed his most frequent 5-behavior sequence "Up-Dive-Surface-Rest-Float" and return to "Up" with an empirical probability of 0.0978 ± 0.03 (2 SE) (Figure 12 and Appendix VII). This means that of all the possible 5-behavior cyclic permuations of 15 behaviors, the elder male performed this one in this order, but starting anywhere in the sequence, approximately 10% of the time. The younger male performed his most frequent 5-behavior sequence "Up-Sink-Whine-Float-Dive" and return to "Up" with an empirical probability of 0.0236 ± 0.006 (Figure 13 and Appendix VIII). This gives a probability of approximately 2%.

Those sequences occurred very infrequently outside the breeding season. For the older male, the probability was $8.5 \times 10^{-6} \pm 1.9 \times 10^{-5}$ (Appendix IX). The sequence that was most frequent during the breeding season for the younger male was never observed outside the breeding season (Appendix X).

The data from observations through the underwater windows showed that the same sequence was the most frequent for the older male (em-

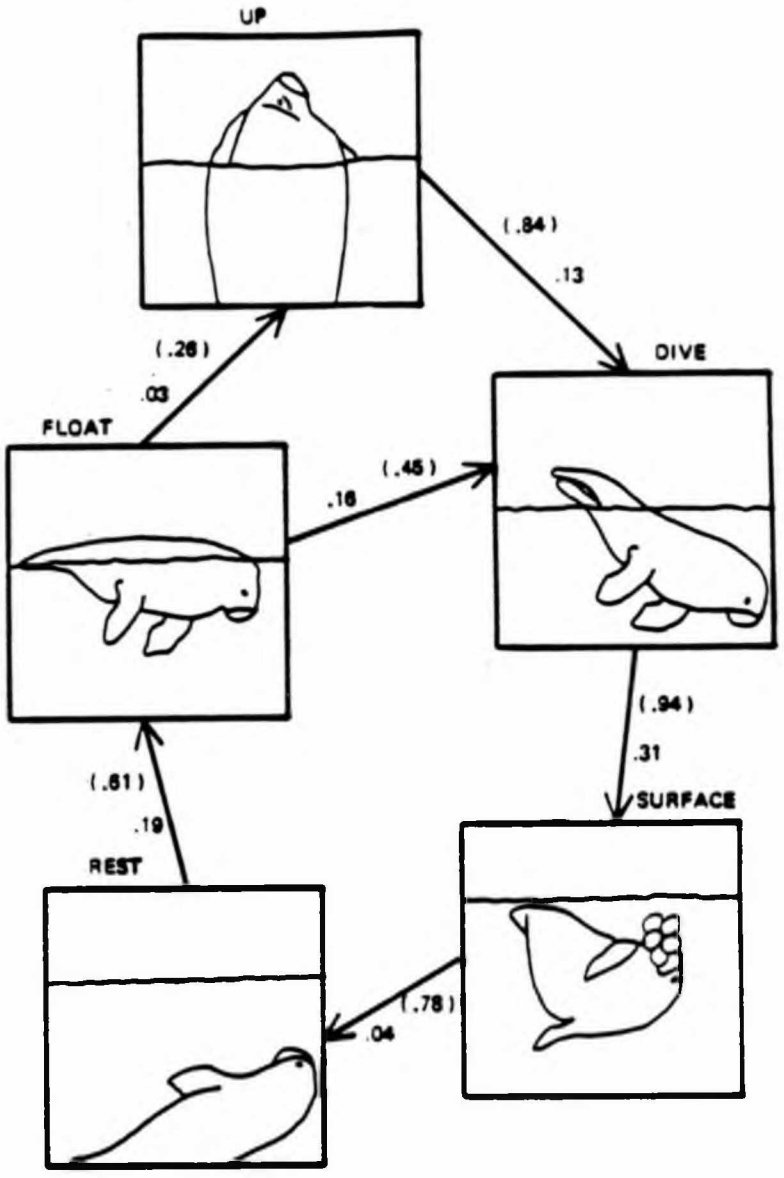


Figure 12. The five behavior sequence (outer ring) with the highest empirical probability of occurring during the breeding season for the older male walrus at Marineland. The transition probabilities between the behaviors during the breeding season (within parentheses) and outside the breeding season (without parentheses) are shown. The empirical probability of this sequence (outer ring) occurring during the breeding season is 0.0978.

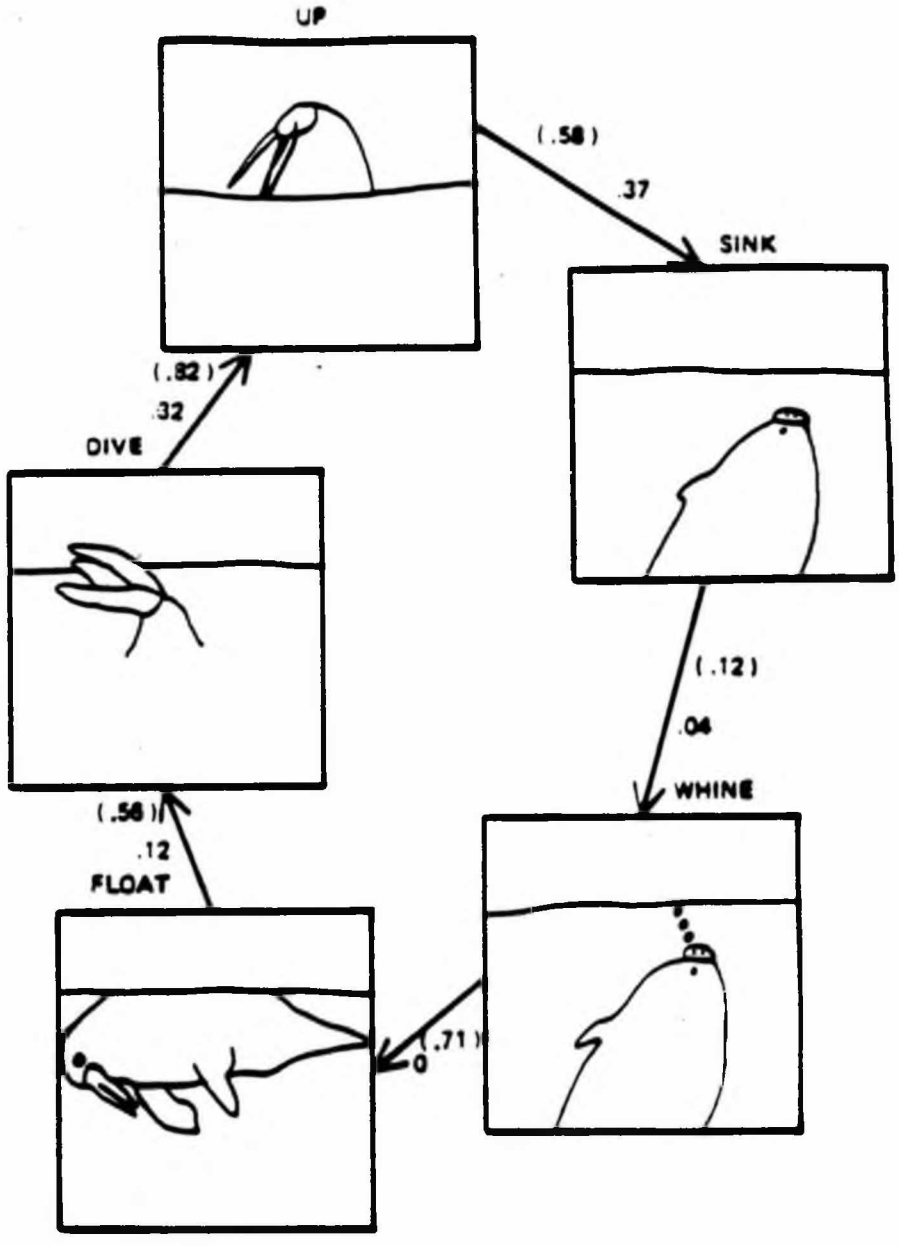


Figure 13. The five behavior sequence (outer ring) with the highest empirical probability of occurring during the breeding season for the younger male walrus at Marineland. The transition probabilities between the behaviors during the breeding season (within parentheses) and outside the breeding season (without parentheses) are shown. The empirical probability of this sequence (outer ring) occurring during the breeding season is 0.0236.

pirical probability = 0.0428 ± 0.01) (Appendix XI). However, for the younger male the sequence "Up-Sink-Bell-Surface-Float" and a return to "Up" was the most frequent, with an empirical probability of 0.0380 ± 0.006 (Figure 14 and Appendix XII).

The displays by the younger male, often appeared to be in several phases. He often initiated his display with a 3-behavior cycle "Up-Splash-Dive", which was often repeated several times. That 3-behavior cycle was perfomed with an empirical probability of 0.0861 ± 0.01 (Appendix XIII). Following that. he often performed the first three behaviors (i.e., "Up-Sink-Bell") of the 5-behavior cycle with an empirical probability of 0.1988 ± 0.02 (Appendix XIV). Occasionally. he repeated that or performed the entire 5-behavior cycle ("Up-Sink-Bell-Surface-Float") (Figure 14).

The difference between the surface and underwater 5-behavior permutations for the younger male appears to have been due to physical problems of observations. I discovered after several weeks that I was able to hear the "Bell" vocalization from above the water only when the ambient background noise was at a low level. Because of this, the complete sequence that could be seen and heard through the underwater windows usually was not evident from above the surface. However, even though the surface observations are less complete, they are the ones that are comparable between the seasons, and as such are essential for a comparison of the behavioral sequencing between the seasons.

The probabilities shown in the transition probability matrix for

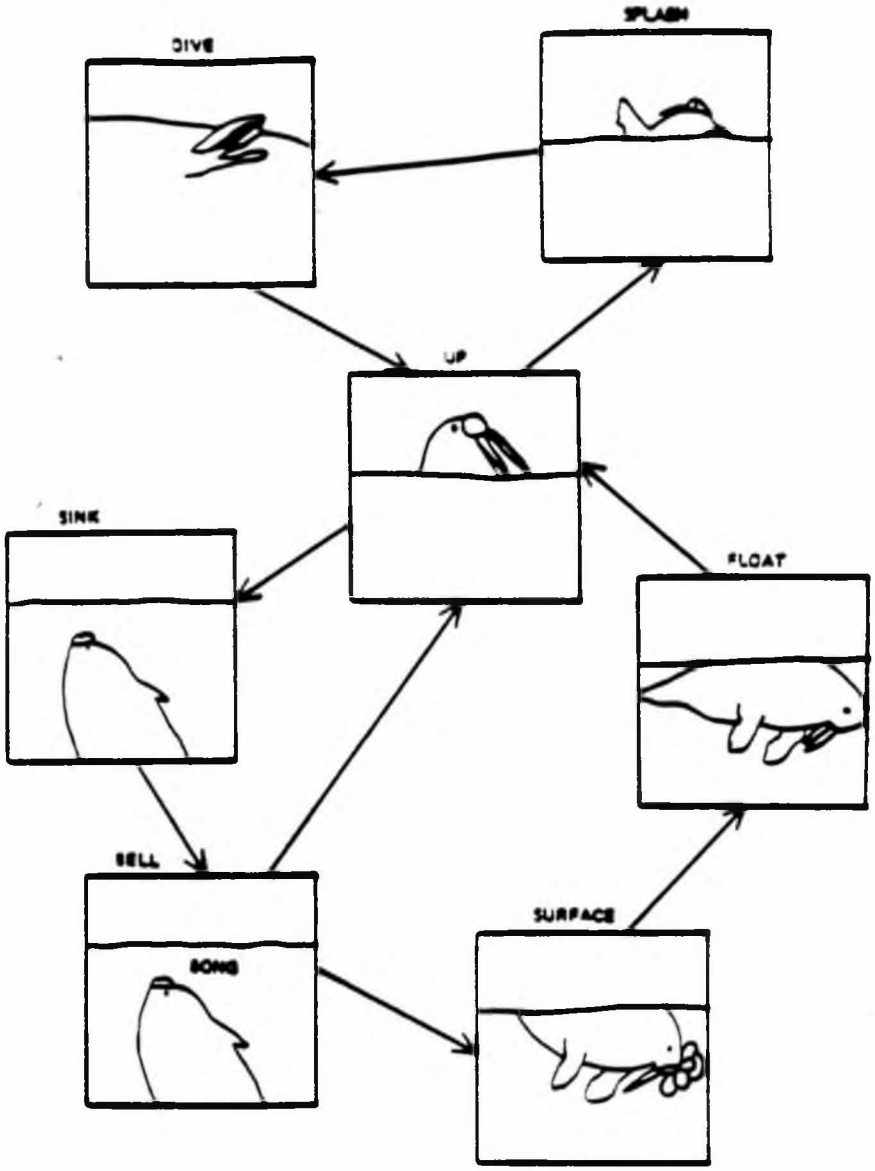


Figure 14. The 3- and 5- behavior sequences with the highest empirical probabilities of occurring during the breeding season for the younger male walrus at Marineland when he was observed through the underwater windows. The empirical probabilities of these sequences occurring during the breeding season are 0.0380 (5- behavior sequence) and 0.0861 (3- behavior sequence, "Up-Splash-Dive") and 0.1988 (3- behavior sequence, "Up-Sink-Bell").

the 5-behavior cycles in Figures 12 and 13 indicate that the weakest link in the older male's 5-behavior cycle was the return from "Float" to "Up" (Figure 12). That is, the probability of each step in the sequence "Up-Dive-Surface-Rest-Float" was high (61% to 94%) during the breeding season, but the probability of return to the start of that sequence ("Up") was low (26%). Frequently, the male by-passed the initial "Up" behavior and continued on with one of the other behaviors.

The breeding season display of the younger male was not as well defined as that of the older male (Figure 13). The probability of each step in the younger male's sequence "Up-Sink-Whine-Float-Dive" varied greatly (12% to 82%) and tended to be lower than that for the older male. The younger male returned to "Up", the initial behavior, more frequently than did the older male.

The 5-behavior cyclic permuations that had the highest probability of occurring during the breeding season are shown in Figures 12 and 13. Also shown on these figures are the probabilities of the transitions from one behavior to another, and of the sequences. both during and outside the breeding season. When the breeding season is compared with the rest of the year. it can be seen that the probabilities of the transitions are greater during the breeding season than outside the breeding season (Older male: 26%-94% vs. 2%-31%; Younger Male: 12%-82% vs. 0%-37%).

Displays usually were performed only by males. but the females

occasionally performed some of the display behaviors. Those displays by females took place throughout the year. The female stationed herself vertically, facing a wall, and spluttered and/or splashed and/or sank. Twenty-five female displays were observed at an overall frequency of 0.2/hr, and their durations ranged from 1 sec to 34 min. (Mean=4 min 58 sec, s.d.=9 min 1 sec). Of these 6 (24%) were followed within one minute by an interaction with the male, and 5(20%) took place during an interaction with the male.

INTERACTIONS

Male - female interactions took place thoughout the year but more frequently outside than within the breeding season (3.02/hr. vs. 2.02/hr., Z test=4.8633, $p<0.001$). For the younger pair, those interactions also were longer in duration outside than within the breeding season (Median=60 sec vs. 31 sec, Mann Whitney U=15,868.0, $p<0.001$, N=260, M=176). For the older pair, also, the interactions tended to be longer outside the breeding season, but the difference was not significant (Median=118 sec vs. 72 sec, Mann Whitney U=1,707.0, $0.1<p<0.25$, M=154, N=23).

Each pair also spent a greater proportion of their time interacting outside than within the breeding season (Younger 11% vs. 7%. $X^2=22.995$, d.f.=1, $p<0.001$; Older 13% vs. 6%, $X^2=42.877$, d.f.=1, $p<0.001$). Their interactions also tended to be more evenly

distributed thoughout the daylight hours outside than within the breeding season (Figure 15). During the breeding season. the older pair tended to spend more time interacting during the late afternoon, and the younger pair during the early morning.

Mounting of the female by the male took place only in the water. While floating, at an angle of about 45°, the male held the female's hips from behind. His head was about the level of her shoulders. and his pelvis curved under hers. positioned for copulation. The same orientation was described for Phoca vitulina by Venables and Venables (1957) and for Leptonychotes weddelli by Cline et al. (1971).

Because most of my observations were made from above the water or through partly murky water, I often could not determine whether copulation took place during mounting. Once while I was observing the animals through the underwater windows, the male walrus mounted the female within 5 m of the window, and the water was clear enough that I saw copulation take place. The male whistled just before the pair separated. Possibly copulation also took place during many of the other mounts that I observed, since the male often whistled before the pair parted.

I observed many displays which did not lead to interactions between the male and the female, and many interactions that were not preceeded by displays (Table 10). I also saw few interactions result in mounting. During the breeding season, interactions were preceeded by displays more often than not (65%, X^2=21.74, d.f.=1, $p<0.001$).

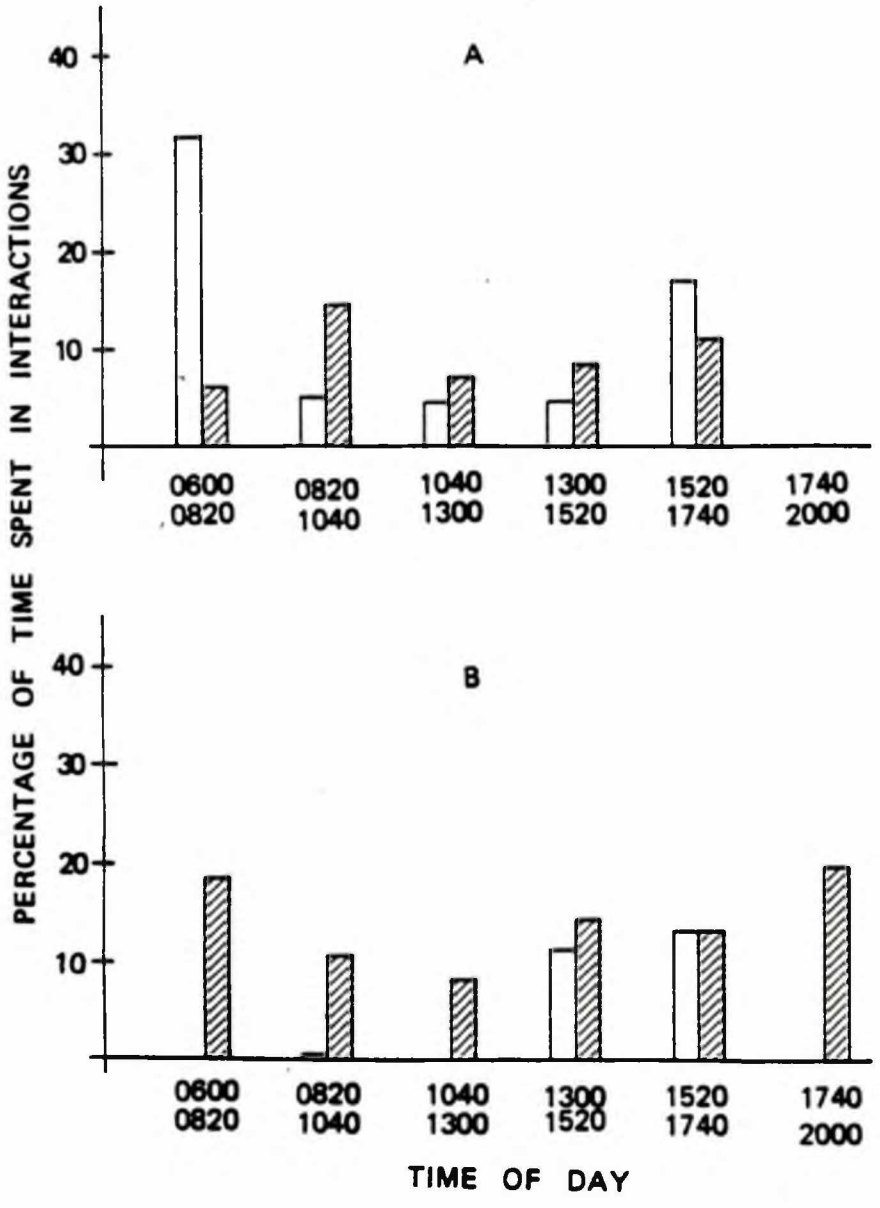


Figure 15. Percentage of time spent by the younger (A) and the older (B) pairs of walruses at Marineland in interactions, within the breeding season (open bars) and outside the breeding season (cross-hatched bars), in relation to the time of day.

Table 10. Relationship between displays, interactions, and mounting.

Event Observed	Within Breeding Season		Outside Breeding Season	
Displays followed by interactions	54/450	12%	362/1005	36%
Interactions preceded by displays	125/193	65%	160/432	37%
Interactions resulting in mounting	10/193	5%	86/432	20%

During the breeding season, interactions within pairs more often were initiated (Binomial Test, $p<0.05$, M=128, N=51) and terminated (Binomial Test, $p<0.05$, M=163, N=26) by the female than by the male. Conversely, outside the breeding season, the male initiated the interactions (Binomial Test, $p<0.05$, M=304, N=103) and the female terminated them (Binomial Test, $p<0.05$, M=226, N=155).

COW - CALF BEHAVIOR

Birth of a calf

I observed the birth of a walrus calf to the younger female at Marineland on 7 June 1981 (Figure 16). I began observations on the day of the birth at 0500h, when the female and her mate were lying side by side, asleep on the platform. At 0557h the female secreted a 10 cm long strand of white mucus from her vaginal opening. The first contraction took place at 0606h, and the female became restless, looked towards her hind flippers, pressed her hind flippers together and stretched. For the next 2.5 hours she was calm, but occasionally vocalized and threatened the male. The release of the amniotic fluid was not observed.

At 0853h, the next contraction began. This time the female stretched and alternately raised her hips and her chest several times. After a vocal threat by the female at 0856h, the male left her side and entered the water. She continued to stretch for a few minutes and

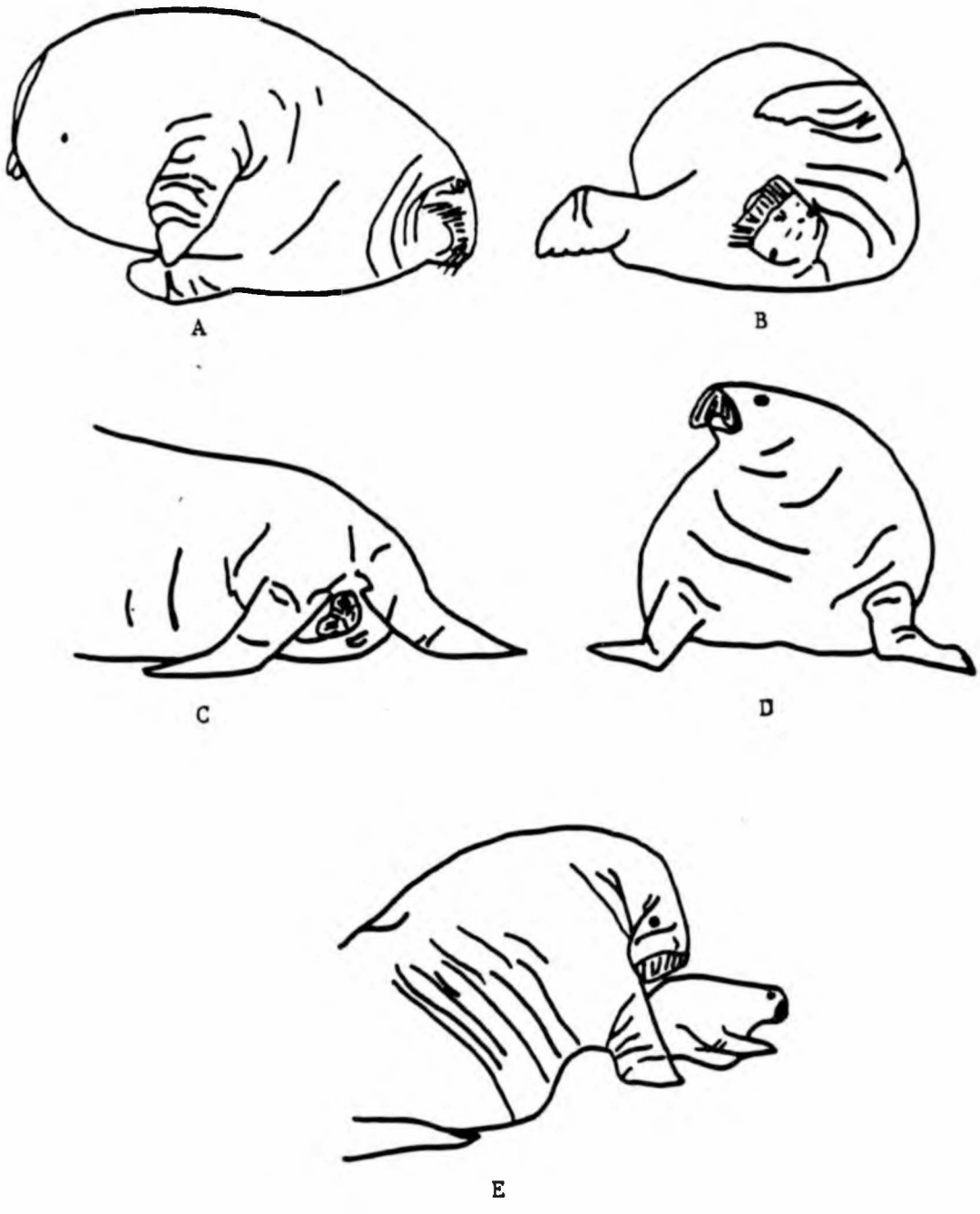


Figure 16. Behaviors that occurred during the birth of a walrus calf. The female walrus rests (A), shifts (B), raises her hips during a contraction and the calf's head appears (C), looks back as the calf is born (D), and looks at the newly born calf (E). The sketches were drawn from photographs.

then lay down again. Observations were suspended from 0900h to 0928h. From 0928h to 0932h another contraction came.

The head of the calf first appeared at 0929h. Between 0936h and 0948h, the female slowly rolled back and forth from her abdomen to her back several times. Another contraction took place between 0950h to 0958h and another from 0959h to 1000h. The cow's final contraction started at 1002h and ended at 1005h when the calf was completely emergent. Severing of the umbilicus was not seen, and delivery of the placenta was not observed.

Immediately, the calf began to bellow; and the female responded at once, turning to touch the calf's head and back with her mystacial pads and nasal region. From 1011h to 1535h, the calf did not vocalize and did not move more than its head. At 1535h, in response to repeated vocalizations from the female, the calf bellowed again. At 1550h the cow pushed the calf into the water and swam, holding it with her foreflippers. The last time the calf breathed was at 1557h. At 1607h, the female released the calf, and it floated to the surface, dead.

Postnatal Behavior

I observed the postnatal behavior of the elder pair and their fourth calf (born in 1982), from the day of its birth until 17 days later.

The calf was active and spent much of its time suckling. The intervals between suckles ranged from less than 10 seconds to 65 min

27 sec, with no apparent arithmetic discontinuity in the frequency of occurrence of intervals of different lengths. The longer intervals obviously were breaks between suckling bouts, but the minimum interval between bouts was more difficult to identify. When I plotted the data semi-logarithmically as frequency vs. duration of the interval, however, a change in the slope of the curve was suggested in the vicinity of 60 seconds (Figure 17). Since that discontinuity indicates a significant change in behavior, I chose one minute as the minimal interval between suckling bouts. All shorter intervals than one minute were regarded as pauses within bouts.

On that basis, I observed all or part of 102 suckling bouts by the Marineland calf. Those bouts took place more often in the morning (0600 - 1040, 1.40 bouts/hour, M=66 bouts) than later in the day (1040 - 2000, 0.78 bouts/hour, N=36 bouts) (Z test=2.9079, $p<0.005$)(Figure 18). The same conclusions were reached when the data were analyzed with respect to individual suckles (Z test=4.02, $p<0.001$). The calf also tended to spend more time suckling in the first two thirds of the daylight hours than in the evening. The average percentage of time spent suckling in the daylight hours was 10% (Figure 19). My data from wild walruses showed a similar proportion: calves spent about 9% (N=3) and the older juveniles about 10% (N=5) of their time suckling in daylight hours.

The frequency of occurrence of suckling bouts and individual suckles decreased from the first to the second week of the Marineland

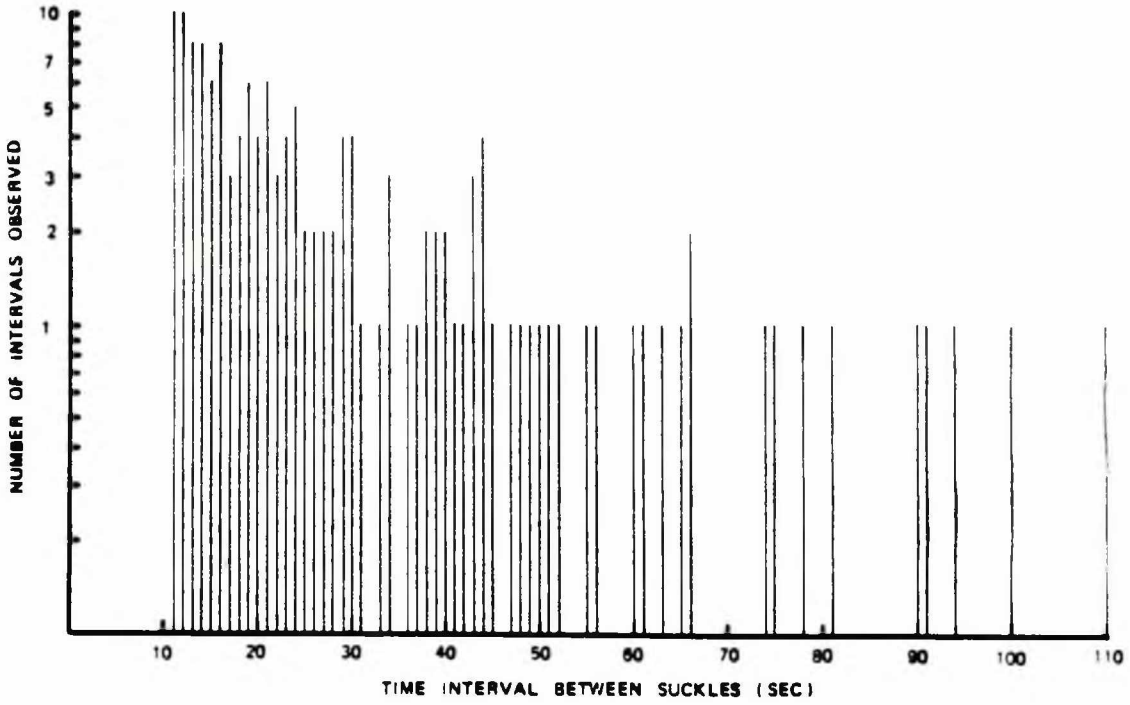


Figure 17. Frequency of occurrence of time intervals of different lengths between suckles. The change in the slope of the curve indicates a change in probability of continuity.

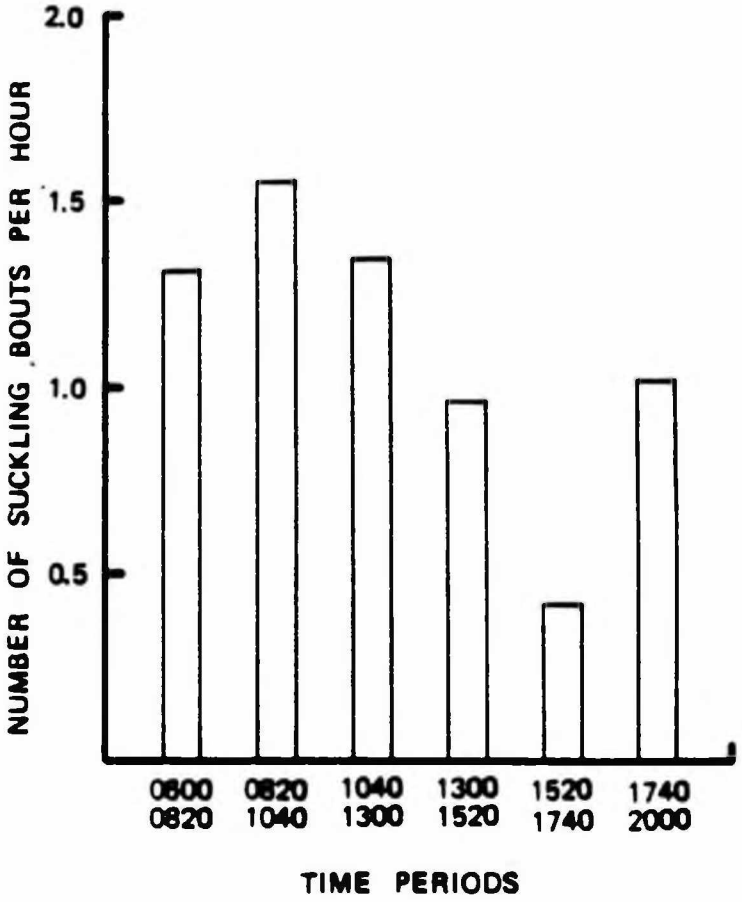


Figure 18. The number of suckling bouts per hour, relative to the time of day.

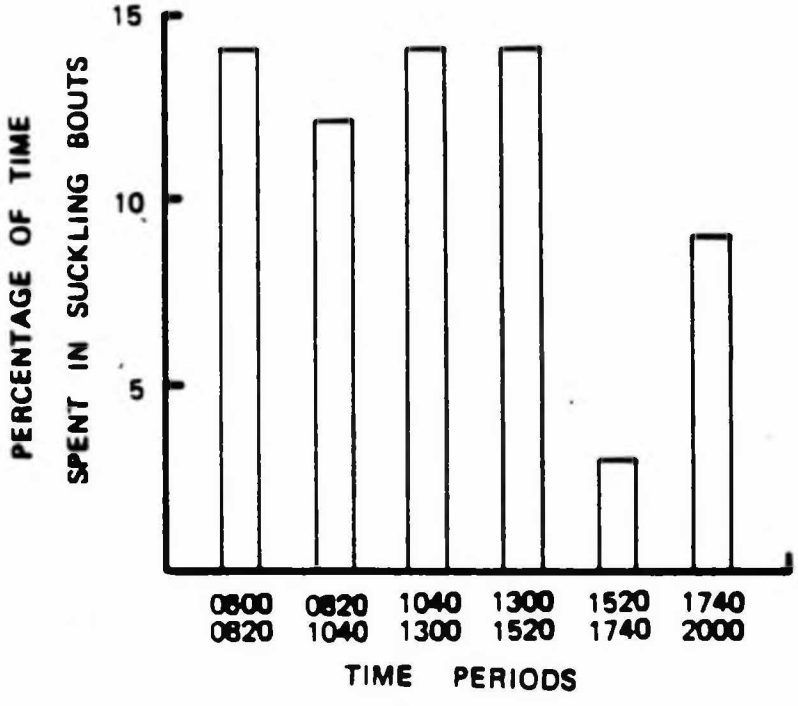


Figure 19. The percentage of time that the calf spent in suckling bouts, relative to the time of day.

calf's life (Bouts; Z=3.99, p<0.001) (Suckles; Z=6.15, M=280, N=171, p<0.001). The average frequency of suckling bouts in the calf's first week was 1.5/hour (N=68), as compared to 0.7/hour (N=33) during second week (Figure 20). The durations of the suckling bouts did not increase during the second week as the bouts became less frequent (Mann Whitney U=0.1665, p>0.50, M=68,N=33). The implication was that the calf had learned to suckle more efficiently by the second week.

The cow and the calf initiated the suckling bouts with nearly equal frequency (Cow=56% vs. Calf =44%; X^2=0.04, p>0.50, d.f.=1, N=90). Many more individual suckles were initiated by the calf than by the cow (78% vs. 22%, Binomial Test, p<0.05, N=413). When a suckling bout was initiated by the cow, she often led the calf by called it with a pup contact call, then rolled onto her side, exposing her nipples (Figure 21). If the calf did not start to suckle, the cow often rolled onto her belly and called or pushed the calf toward her abdomen as she exposed her nipples again. The calf initiated suckling bouts by approaching the cow and vocalizing, while rubbing the cow's side with its vibrissae. The calf continued vocalizing and rubbing until the cow rolled onto her side, exposing her abdomen (Figure 22). Then the calf rubbed the cow's belly with its vibrissae until it found a nipple, whereupon it began to suckle.

The calf appeared to initiate suckling bouts when she was hungry; the cow apparently terminated them when she had no milk left. The suckling bouts initiated by the calf were longer than those initiated

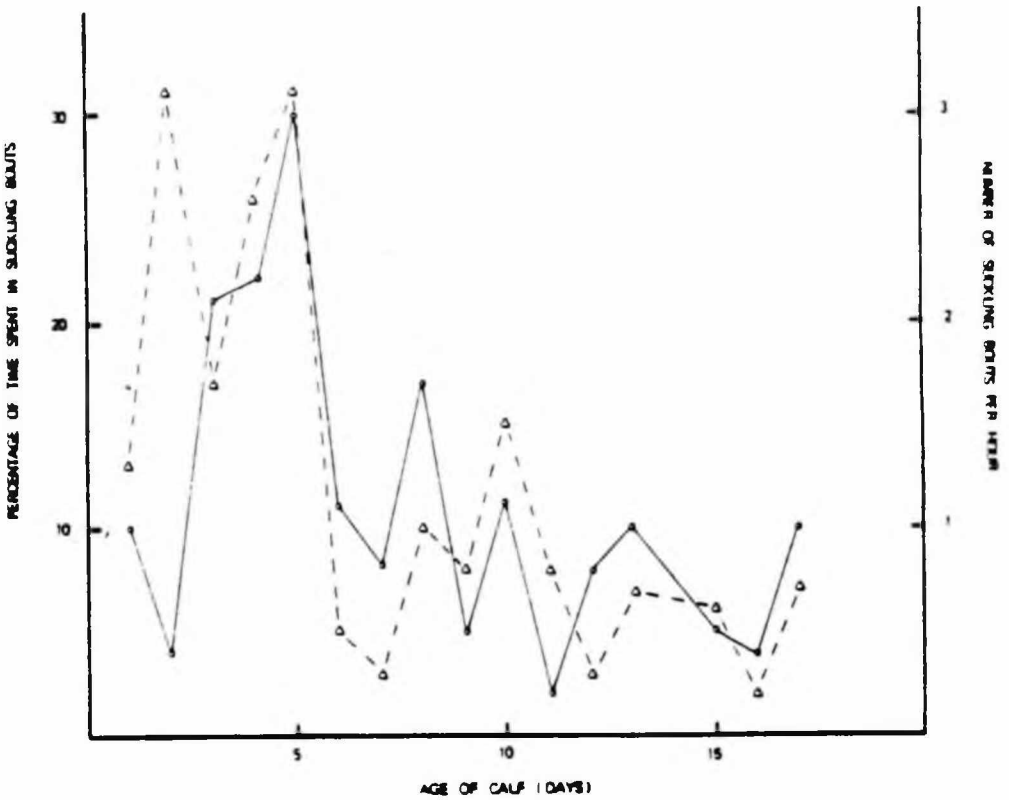


Figure 20. Frequency of occurrence of suckling bouts (———) and percentage of time spent per bout (— — —), relative to the age of the calf.

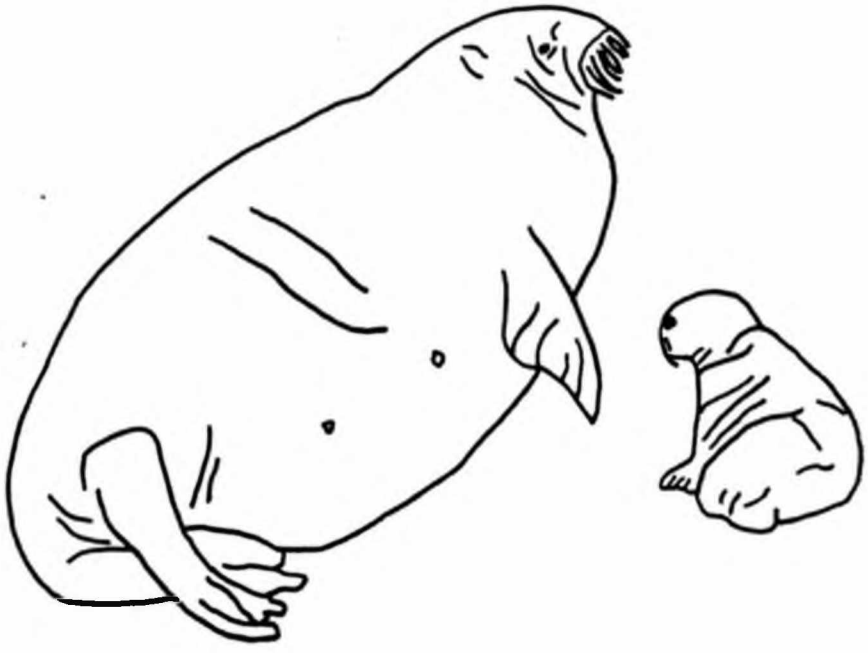


Figure 21. Female walrus exposing nipples when initiating a suckling bout.

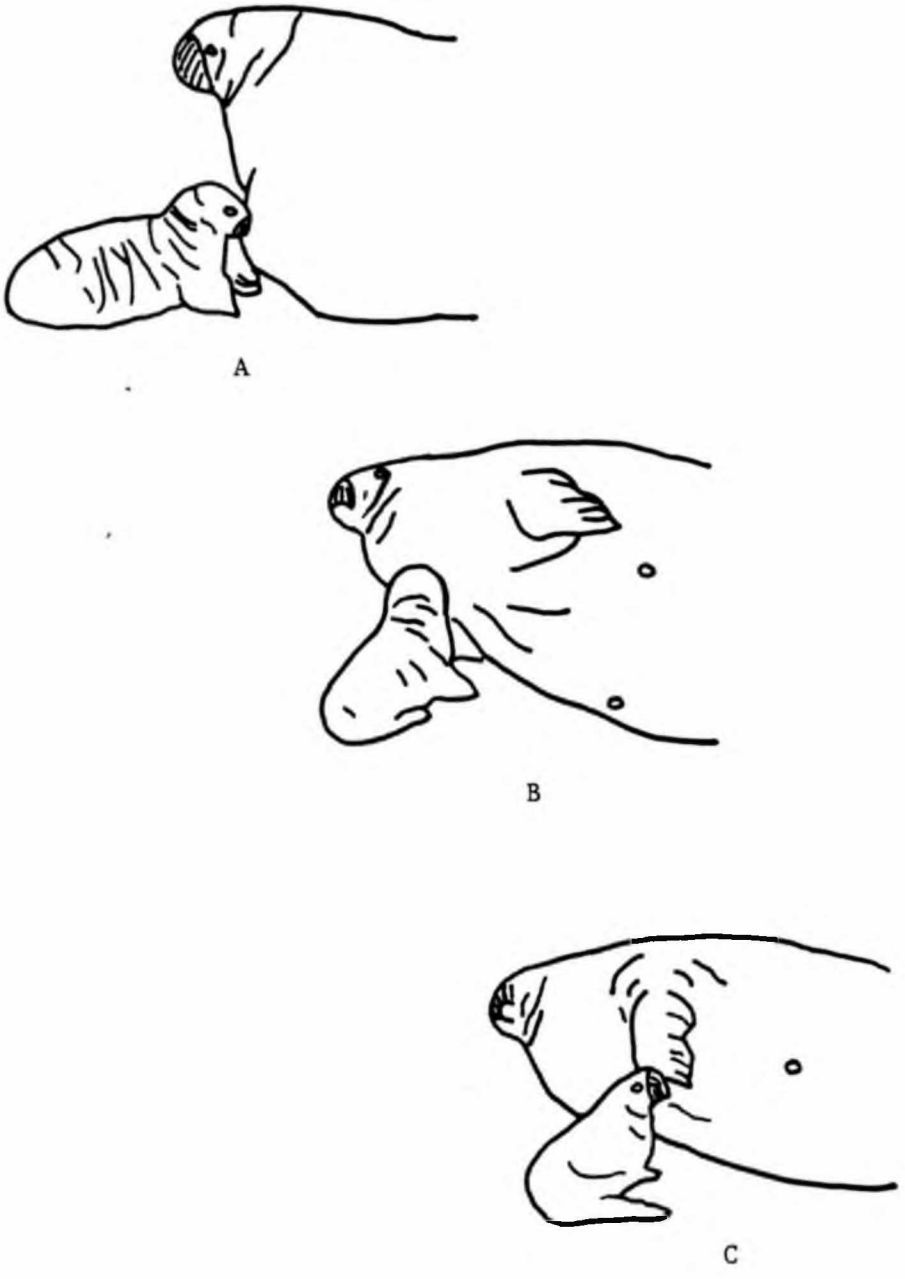


Figure 22. Steps in the calf's initiation of a suckling bout. The calf approaches the female and touches her side (A). The female rolls onto her side and exposes her abdomen; the calf watches (B). Calf begins to search for nipples (C).

by the cow (Mean=7 min 10 sec for the calf, vs. 4 min 39 sec for the cow, Mann Whitney U=1.83, $0.025<p<0.05$, M=37, N=48), but the bouts terminated by the cow were longer than those terminated by the calf (Mean=7 min 15 sec vs. 5 min 16 sec, Mann Whitney U=1.6549, $0.025<p<0.05$, M=23, N=58). The calf terminated more suckling bouts and individual suckles than the cow (Bouts 72% vs. 28%, Binomial Test, $p<0.05$, N=94)(Suckles 87% vs. 13%, Binomial Test, $p<0.05$, N=413). The male caused termination of a few suckling bouts (4%, N=98), by disturbing the pair.

In 9 hr 53 min 8 sec of observed suckling, the calf assumed the reverse parallel position in 59% of the bouts, perpendicular position in 36% of the bouts, and direct parallel position in only 5% of the bouts.

From the start of my observations, the calf was active and the cow and calf interacted both tactually and vocally. They were together (i.e., less than one calf-length apart) most of the time but they separated occasionally. The calf did not appear to orient toward the cow or to react to her vocalizations during the first two days; later, the calf appeared to be more responsive. However the data are inconclusive. During the first 2 days the calf left the cow (17 times), which is more often than the cow left the calf (11 times). Later, the cow appeared to leave the calf more frequently (151 times) than the calf left the cow (134 times). However, this difference is not significant ($X^2=1.916$, d.f.=1, $p>0.05$). A Chi-squared test of the

frequency of approaching indicated that the cow tended to approach the calf more often (19 times) than the calf approached her (10 times), during the first two days, and that after the first two days, the calf approached the cow more often (170 times) than the cow approached the calf (114 times, X^2=6.934, d.f.=1, p<0.010).

Overall, the calf initiated separations by moving away from the cow about as often as the cow moved away from the calf (49% vs. 51%, Binomial Test p>0.05, N=313). However, the calf aproached the cow more often than the cow approached the calf (58% vs. 42%, Binomial Test p<0.05, N = 313). From the overall leave/approach matrix, I found that the cow approached when the calf left (120/151) and the calf approached if the cow left (149/162); that is, they appeared to follow each other rather than to separate (X^2=159.89, d.f.=1, p<0.001).

When the calf left and the cow approached, the average separation was 7 sec. This was a significantly longer interval than when the cow left and the calf approached (Mean=4 sec)(Mann Whitney U=2.37, 0.005<p<0.01, M=83, N=86). This suggests that the calf tended to maintain the proximity rather than the cow.

To further examine the roles of the cow and calf in maintaining closeness to one another, I calculated the proximity quotient for the calf (Hinde 1974). The percentage of times when the calf left the cow (48.9%) was subtracted from the percentage of approaches by the calf (58.1%) in 313 observations. Since the resulting proximity quotient (+9.2%) is a positive number, the calf was most responsible for

keeping the pair together.

Vocalizations by the cow when the pair was apart were very important in reuniting them. Many times, Russell (1976) and I observed that the cow moved away from the calf, looked back at it, and vocalized. If the calf did not approach her, she returned to it, vocalized near its head, and withdrew again. This was repeated until the calf approached her. Because of this, I felt that some of the approaches by the calf could be attributed to the cow, since her vocalizations appeared to have coaxed the calf to approach her. On that basis, I recalculated the proximity quotient by subtracting the proportion of "leaves" by the calf from the proportion of "approaches", less those instances in which the cow vocalized. The result (30.3% - 48.9% = -18.6%) is a larger negative value than for the cow, which indicates that the cow may have been most responsible for maintaining proximity between the pair, and that she may have done this in part by means of her vocalizations.

I compared the time interval between the calf's bellow and the cow's approach (Mean=5.38 sec, N=5) and the interval between the cow's pup contact call and the calf's approach (Mean=24 sec, N=92). Although the cow appeared to respond much faster to the calf's vocalizations, than the calf did to hers, the difference was not significant (Mann Whitney U=1.56, $0.10<p<0.05$, M=5,N=92).

When the calf left, the female either followed it (55%) or gave a pup contact call (44%, Binomial Test, $p>0.50$, N=151). After the cow

vocalized, the calf either returned to her (46%). or the cow followed the calf (54%, Binomial Test, $p>0.50$, N=67). When the cow left, the calf quickly followed her (53%) or the cow gave a pup contact call (45%, Binomial Test, $p>0.50$, N=162). If the cow vocalized, the calf usually followed her (85%, Binomial Test, $p<0.05$, N=73).

The calf was inactive or recumbent and apparently sleeping much more of the time in the afternoon and evening than in the morning (Figure 23). Overall, it was inactive 42% of the time (N=94 hr.). From observations of wild walruses, I found that the wild calves were inactive 58% of the time (N=11 hr.) while they were on ice floes; older dependents (1-3 yr. olds) were inactive 50% of the time (N=20 hr.).

The Marineland calf spent very little time interacting with the male (1.4%). Those interactions took place more frequently and occupied a greater proportion of the calf's time early in the morning (Figures 24,25) than at other times.

The mean duration of 134 interactions between the calf and the male was 36 seconds. Forty-eight (36%) of those interactions included direct threats by the male to the calf; the remaining 64% involved naso-nasal greetings, and facing away by the male and one-way olfactory-tactual investigations by the calf. Of the direct threats to the calf, 31% were strikes. 56% were physical contacts (pushes, flippering), 9% kinesic tusk threats, and 4% vocal threats. Overall. the calf was struck in 11% of the 134 encounters with the male.

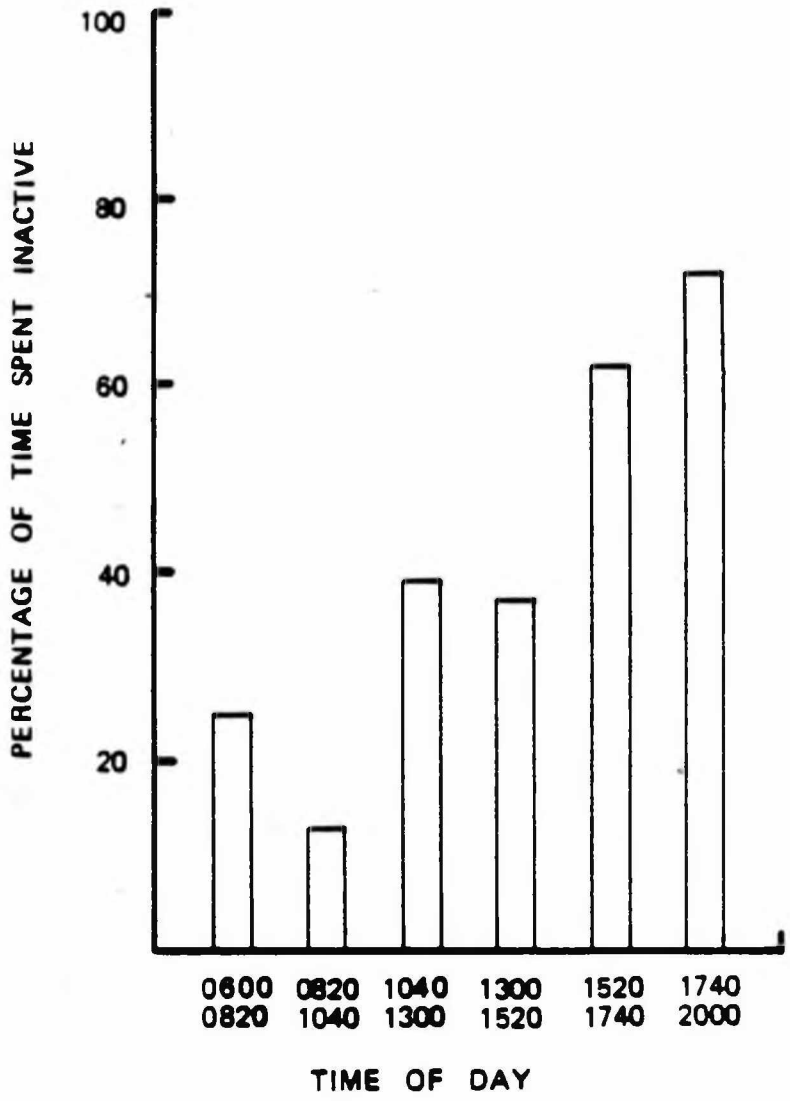


Figure 23. Percentage of time that the Marineland calf was inactive in relation to the time of day.

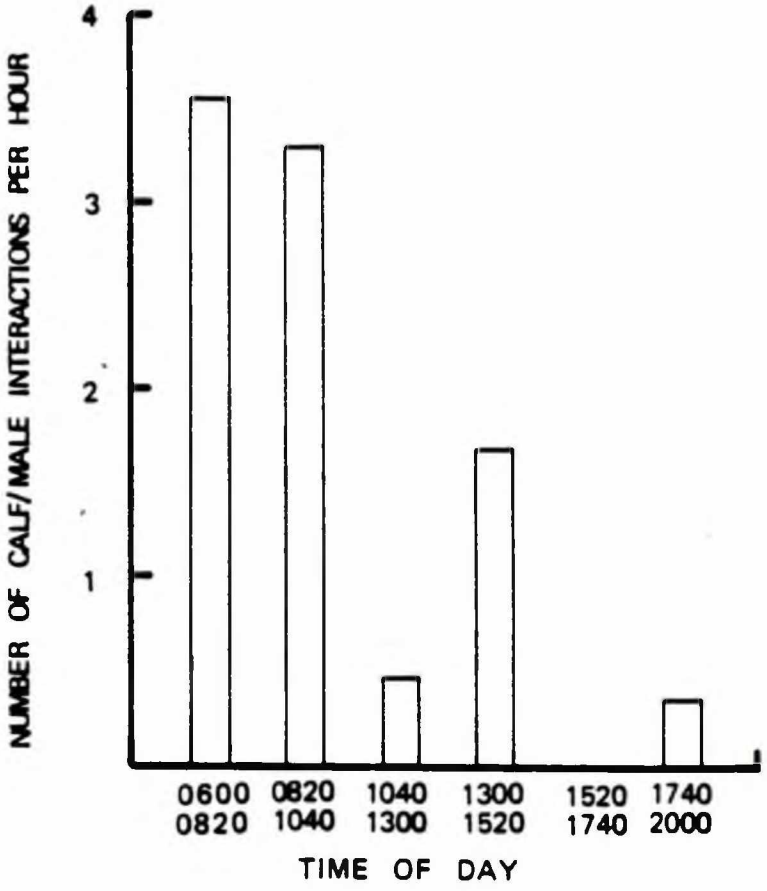


Figure 24. Frequency of calf/male interactions relative to the time of day.

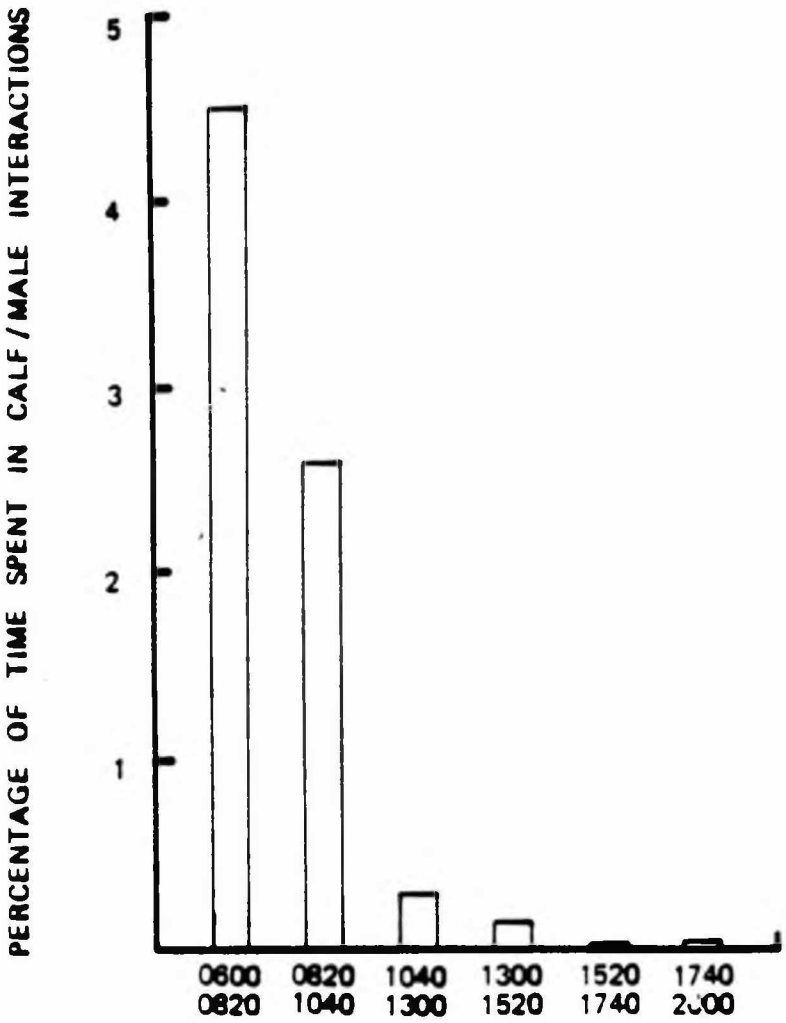


Figure 25. Percentage of time that the calf spent interacting with the male in relation to the time of day.

The male's threats to the calf were immediately preceeded 31% of the time by the male approaching the cow and calf, 33% by the calf approaching the male, 15% by a male/female interaction, and 21% while all individuals were resting. The female responded to the male's aggression toward the calf in an average of 4 seconds. She responded 41 out of 48 times (85%) overall and every time when the calf vocalized (N=6). The female's most frequent response was a vocal threat (44%). In addition, she responded with kinesic tusk threats (10%), physical contact (pushes, flippering) with the male (6%), tusk strikes (4%), calling the calf (21%), or did not respond at all (15%). In the presence of the calf, overall, the female threatened the male more frequently than he threatened her (Binomial Test, $p<0.05$, N=572, 289). However, during the second week the frequency of threats by the male increased from 2 threats/hour to 4 threats/hr (Z test=6.2433, $p<0.001$), while the female threatened at a constant rate of 6 threats/hr (Z test=0.92, $p>0.05$).

Wild female walruses threatened other animals less frequently than the captive female threatened the male. Wild females with 2.5 month old calves threatened other animals 0.77 times per hour, and those with older juveniles, threatened other animals 0.49 times per hour. These threats included static and kinesic tusk threats, tusk strikes and physical contact (pushes, flippering).

In male/female agonistic encounters in the presence of the calf (N=164), the cow vocalized threats in many more of the encounters than

did the bull (84% vs. 7%, X^2=63.418, d.f.=1, p<0.001). She vocalized more frequently in each encounter than did the bull (Mean=2.1 vs. 0.1). The cow also gave kinesic tusk threats (KTT's) in more encounters than did the male (37% vs. 16%, X^2=7.301, d.f.=1, 0.010<p<0.005), although the mean number of KTT's per encounter for the female and the male were similar (0.7 vs. 0.2). Both the cow and the bull struck the other in approximately the same number of encounters (13% vs. 17%, X^2=0.508, d.f.=1, p>0.10), and they struck with a mean number of 0.2 and 0.4 strikes per encounter. Physical contact (pushes, flippering) was used as a threat by the female and the male in a similar proportion of encounters (17% vs. 18%, X^2=0.34, d.f.=1, p>0.10).

DISCUSSION

Walruses mostly reside far from shore in ice covered arctic waters throughout the year. To study their behavior under natural conditions, therefore, is difficult and has been attempted infrequently. Because of the unfavorable (for the observer) environment of the walrus, many problems arise when attempting to observe the animals in the wild, For example, subtle behaviors and vocalizations that play critical roles in the walrus' social system may not be detectable under some field conditions. To avoid those difficulties and to monitor individual walruses through seasonal and age-related changes in behavior, I aimed this study mostly at walruses reared in captivity at Marineland in Los Angeles.

The question of how captivity might have affected their behavior cannot be answered fully, but this and other studies have shown that the life history of captive walruses is biologically similar enough in most ways to that of wild walruses that fundamental similarities in behavior also are probable.

Both captive and wild walruses breed in January and February, calve in May and June, and molt during the late spring and summer (Fay 1982). The wild males are capable of first breeding at 10 years of age, and the two pairs of walruses in this study also first bred successfully during their 10th year. Although some wild females are

capable of breeding as early as their fourth or fifth year (Fay 1982), their reproduction in Marineland apparently was delayed by the slower sexual development of the males.

The captive environment, however, imposes some clear constraints on the behavioral development of the walruses that have been taken into account in this study. The walruses at Marineland were reared in captivity since infancy. Therefore, they did not have the opportunity to learn behaviors from their parents or other adults. And because the pairs were housed separately after reaching maturity, they were unable to interact and learn from each other. With those limitations, I have examined only the more instinctive aspects of their behavior and have interpreted those with caution.

ENERGY INTAKE

The Marineland walruses consumed vastly different amounts of food at different ages, as well as in relation to the season and to their reproductive status. Comparable variations in food intake have been suggested by findings in other studies of both wild and captive walruses.

Fay (1982) summarized the imformation available on food intake by captive walruses, mainly from data presented by Reventlow (1951), Bridges (1953), Hagenbeck (1963), and Brown and Asper (1966). That information was from seven different walruses that were 1.5 to 7 years

old, and were reared in five different zoos and aquaria, whereas in this study, I examined intakes for six animals that were 2 to 21 years old and all reared in the same aquarium. This new information compares favorably with the earlier reports, and it provides some further understanding. For example, it indicates that although walruses consume more energy as they grow older and larger, they consume less per unit of body mass. Fay (1982) stated that his estimated mean caloric intake for "metabolic size" (380 kcal/$kg^{3/4}$ TBW) was applicable to all ages since the data available to him did not indicate any change with age. Fedoseev (1976) suggested that, although food intake with respect to body weight decreases with age for most pinnipeds, walruses appeared to consume food at a steady rate with respect to body weight at all ages. This study, which dealt with a much larger volume of data from a few individuals over many years of their lives, showed a range of intakes, however, in which the lowest values per unit of body weight were the maintenance levels for the oldest adults, and the highest values were for the youngest, growing juveniles. That is, not withstanding Fay's (1982) and Fedoseev's (1976) assumptions to the contrary, the intake rate per unit weight is not the same at all ages. Kleiber (1961) reported similar results for other animals.

The adult male walruses at Marineland consumed fewer kcal/day during the breeding season than at other times of the year. Fay (1982) discussed a similar decrease in food intake of wild male walruses during the breeding season. A decrease in consumption by adult

males of other pinnipeds during the breeding season also has been reported (Bartholomew 1970). These include northern fur seals (Bartholomew and Hoel 1953), Steller sea lions (Spalding 1964), southern elephant seals (Ling and Bryden 1981), and grey seals (Bonner 1982).

Whereas the wild male walruses may need to fast for long periods of time, in order to maintain their mobile territories near the estrous females (Fay, Ray and Kibal'chich 1984), the Marineland males had no such necessity. Nonetheless, they still decreased their intake dramatically for several months during the breeding season. Following that period of reduced intake, they increased their consumption steadily until the following winter. Wild male walruses also feed intensively throughout the summer and autumn and tend to be fattest in early winter (Fay 1982).

The walruses at Marineland appeared to consume less food during the molt (June - August) than at other times, but a consistent pattern was not evident. A decrease in consumption during the molt has been described for phocid seals (McLaren 1958; Mansfield 1967). The intake of the Marineland males, especially. tended to decrease in summer following the birth of a calf, but that decrease probably was an artifact of captivity. At the time of calving and for several weeks thereafter, the pool was drained and the adults and their newborn calf resided on the floor of the dry pool. Fay and Ray (1968) found that captive and wild walruses spent most of their time in the water and refrained from hauling out when the temperature was high. It is

possible that the metabolic rate of the captive males decreased at this time because they were unable to retreat from the heat to the cooler water. A decreased metabolic rate has been correlated with high environmental temperatures in many animals (Kleiber 1961).

The energy consumption of nonpregnant, nonlactating adult female walruses at Marineland was comparatively constant, like that of the juvenile animals. This corresponds well to the Eskimos' observation (as reported by Fay and Kelly 1980; Fay 1982) that the fatness of females is comparatively uniform except in pregnancy. The nonpregnant Marineland females, however, did show a marked fluctuation in energy consumption, amounting to a brief period of fasting, in January or February. Since the wild females tend to ovulate in January and February, and because each of the Marineland females became pregnant following such fasts, this coincidence appears to be more than chance. That is, the brief fasts of the captive females appear to have been linked with estrus. That is supported further by the fact that the males also fasted at that time. Furthermore, the same kind of brief fasts by both the females and the males took place often about 1.5 months after the birth of a calf, coincident with the time of post-partum estrus (Fay 1982).

During pregnancy, there are increased energy demands on the mother as the fetus develops (Kleiber 1961). Some mammals compensate for this by reduced activity (Brody 1945); female pinnipeds, including walruses, apparently increase their consumption of food, for they

become obese before the time of birth. The female walruses at Marineland consumed 40 - 50% more energy while pregnant than they did when not pregnant or lactating. They also consumed 50% more during lactation than they did when not pregnant or lactating. Lactating female grey seals, who suckle their pups for a much shorter time, only 18 days, consume up to 6 times more energy per day than nonlactating female grey seals (Fedak and Anderson 1982). Lactating females in some other mammalian species have been found to increase their intake 1 to 2 times when compared with nonlactating females (Kleiber 1961). On that basis Fay (1982) estimated that female walruses that were pregnant and lactating simultaneously might consume up to 100-200% more than a nonpregnant, nonlactating female would consume. The results from the Marineland captives suggest that a 95-100% increase may be more realistic for concurrent pregnancy and lactation in walruses.

For several days before and during calving, the female walruses at Marineland decreased their intake of food. Females of several other pinnipeds also decrease their consumption for one to several weeks at the time of birth. Those pinnipeds include the northern fur seal (Bartholomew and Hoel 1953), the Steller sea lion, and the harbor seal (Spalding 1964). After the birth, the Marineland walruses increased their intake slowly but did not return to a steady state, at or near the nonpregnant, nonlactating level, for several weeks. Wild female walruses also tend to eat very little when they have newborn

calves (Fay 1982). That decreased intake immediately after calving may enable wild females to spend more of their time tending their calves, increasing the calf's chances of survival. The calves also may not be capable of deep or prolonged feeding dives until they are a few weeks old.

Fay (1982) suggested that the most critical time for shortages of food for wild walruses might be in the winter, when the males and females are in the same geographical areas, whereas they are segregated during most of the rest of the year. My data from the Marineland walruses, however, suggest that the highest intakes by both the adult males and pregnant and lactating females are during the autumn (September - December). At that time, the wild male and female Pacific walruses may be in the same geographical areas, but space is not a limiting factor, and the food resources available to them may be greater than in any other season.

BREEDING BEHAVIOR

The male walruses at Marineland displayed in the water at the front corners of their enclosures, beside walls that rose 2 m above the water's surface. Sexually mature male walruses in the wild display in the water beside ice floes where the estrous females are resting (Fay, Ray and Kibal'chich 1984). In the spring and summer, subadult males display in the water alongside a chunk of ice (Fay,

pers. comm.) or a "rock outcrop, cliff face, overhang or boulder" (Miller 1975b).

Unlike the wild adults, the captive adult males performed their display behaviors throughout the year. Nonetheless, they spent more of their time displaying, performed more displays per hour, included more behaviors per display, and the displays were more stereotyped during the breeding season. The displays performed outside the breeding season lasted longer, were less intense, less stereotyped, and the less active behaviors were performed more frequently.

The results from the two captive adult male walruses cannot be used to extrapolate to all wild walruses, but they do appear to support Miller's (1975b) observations. Miller (1975b) found that the displays by subadult males were incomplete and non-stereotyped during the summer, even though they included behaviors and vocalizations similar to those used by the mature bulls in their displays during the breeding season. The displays of wild adult male walruses during the breeding season are strongly stereotyped; the same behaviors are repeated in the same order continually (Ray and Watkins 1975; Fay, Ray and Kibal'chich 1984).

Tinbergen (1952) discussed the question of whether reproductive behavior and displays are innate. "Many of these behavior patterns need not be learned, but are entirely or largely innate; they are often performed in full by individuals reared in isolation, who cannot have had opportunity to learn them" (p. 1). Much of the reproductive

behavior of the walrus appears to be innate. Walruses that were reared in captivity since infancy perform displays during the breeding season that contain some identical behaviors and some very similar behaviors to those performed by wild walruses. There is no possibility that the captive walruses ever saw displays by wild walruses.

The displays by the captives are performed in patterns, but the sequences of behaviors are different and may be less stereotyped than those of wild walruses. However, it should be noted that since the wild courtship displays have not been statistically analyzed, it is unknown to what degree they are stereotyped. Although the male walruses in captivity performed the same vocalizations as the wild bulls, they did not incorporate them into their most frequently performed display sequences. This implies that the sequences of behaviors in the displays and some of the behaviors of wild walruses are learned from other males and that the stereotypy may be reinforced by their competition with others for display stations.

The intensity with which the two captive males displayed and the responses of each to the displays of the other. whom they could only hear and not see, indicated that the motivation to compete is innate and very strong. Agonistic interactions between wild adult bulls during the breeding season can be very intense, and the resulting injuries can be very severe (Fay, Ray and Kibal'chich 1984). This suggests that male walruses actively compete for their display stations and the resulting proximity to estrous females (Fay, Ray and

Kibal'chich 1984). Aggressive competition between adult male Weddell seals (Leptonychotes weddelli) has also been observed during their breeding season. when they actively compete for positions near the estrous females (Mansfield 1958b; Smith 1966).

Copulation by walruses has been observed in the wild, but never during the actual breeding season. Reported matings, summarized by Fay (1982) took place between April and November. The scarcity of sightings of male/female interactions and copulations during the winter is a direct result of the inaccessibility and logistical difficulties in observing walruses at that time of the year. Fay and Ray (1979) and Fay, Ray and Kibal'chich (1984) surmised that copulations took place during the underwater interactions between females and displaying males that they observed in March. All of the copulations that I observed at Marineland took place in the water.

The walruses that I observed at Marineland mounted and probably copulated at least in January, February, March, June, and July. That they copulate throughout the year has been reported previously (Fay 1982). More displays were followed by interactions with females outside the breeding season than within it. However, more interactions were preceded by displays during the breeding season than at other times of the year. During the breeding season, each male performed many displays before an interaction with the female took place.

INTERACTIONS

Male/female interactions at Marineland outside the breeding season were very different from those during the breeding season; more time was spent interacting, interactions were more frequent and lasted longer, and more interactions resulted in mounting. Those findings were quite the reverse of my predictions. Since the pairs at Marineland are always together, however, interactions take place that are not related to breeding behavior. Because of this artifact of captivity, I am uncertain whether this information from captive animals is relevant to the behavior of wild walruses. Also most wild male and female walruses are separate except during the breeding season, so they cannot interact. Because the breeding behavior of wild walruses has been observed very little, the proportion of male/female interactions under natural conditions that lead to actual copulation is unknown.

During the breeding season, Fay, Ray and Kibal'chich (1984) observed that females initiated interactions with the male by joining him in his display station and terminated them by withdrawing to the herd on the ice floe. The females at Marineland also initiated and terminated most of the interactions by approaching and withdrawing from the males during the breeding season. These observations support the hypothesis suggested by Fay and Ray (1979) which said that the mating system of walruses resembles a lek system. At other times, the captive males initiated the interactions, and the captive females ter-

minated them.

COW / CALF BEHAVIOR

Birth of a walrus calf has been recorded only once in the literature. R. A. Ryder (in Fay 1982:202) observed a female giving birth on an ice floe. He described the situation.

> "She sat more or less upright on her front flippers with her body at right angles to the ship, distance approximately 300 yards. The posterior portion of her body was turned somewhat laterally with the ventral side away from the ship. When first seen, the calf was partly visible, steaming and wet appearing. As the ship continued to approach, the female squirmed occasionally and looked back at the newborn calf which gradually became more visible. It lay motionless for a minute or so until the mother saw the ship and slid into the brash. The parent promptly surfaced close by the floe and looked at the calf. It slowly wriggled to the edge of the floe and fell in the brash and water. The cow dived with the calf under her head and tusks. No sounds were heard from the cow or calf and no umbilical cord attachment or actual severing of same by the female was observed".

This event was very similar to the birth that I observed in June 1981 at Marineland, except in that instance vocalizations appeared to have been important. Mechanical noise from the ship may have prevented Ryder from hearing vocalizations between the cow and the calf following the birth. Neither Ryder nor I observed the umbilical cord being severed.

Under natural conditions, pregnant cows at full-term often withdraw to an ice floe at some distance from other cows with young, when they are ready to give birth (Fay 1982). The female that I observed giving birth in June 1981 at Marineland showed a similar tendency for isolation. She became increasingly aggressive toward the male as her contractions became more frequent. Then, one half hour before the calf's head first appeared, she vocally threatened the male, who had been resting beside her on the deck. He immediately withdrew to the water and did not return until after the calf was born.

The remnant of the umbilical cord can persist in wild calves as long as two months (Nikulin 1941). The calf that I watched at Marineland in June 1982 lost its cord within one week.

The calf that I observed at Marineland spent 42% of its time inactive, and the wild dependent young that I observed on the ice spent 52% of their time inactive. These values are much lower than the 95% inactivity reported by Salter (1978) for wild adults hauled out on shore. Miller and Boness (1983) stated that adult walruses are recumbent most of the time that they are on land. However, they did mention that social activity levels of dependent young appear to be higher than for adults. My data support that observation.

The calves born at Marineland began suckling for the first time within 6 to 19 hours after birth (Russell 1976; B. Andrews, A. Soric, pers. comm.). The calf that I observed in 1982 also began suckling before it was 6.5 hours old (A. Soric, pers. comm.).

Walruses spend at least one third of their lives in the water (Fay and Ray 1968), and for that reason, aquatic nursing is important (Miller and Boness 1983). Russell (1976) reported that a calf at Marineland was suckling underwater as early as 7 days after birth. In July it suckled equally on land and in the water, and by August most of its suckling was done in the water. During underwater suckling, the female was in the "Up" position, and the calf was in the "Reverse Parallel" position, vertically upside down in front of her (Russell 1976). This orientation of the female also was described by Loughrey (1959) and by Miller and Boness (1983) as "Bottle".

Before mid-July, the mother and calf also slept mostly on the deck; after that time, they slept in the water most of the time (Russell 1976). When sleeping in the water, the cow most commonly floated in a prone position with her nostrils above the surface. The calf floated parallel to her, within 1/3 m of her side. The calf slept holding it's breath for 2 to 4 minutes. after which it gasped, lifted its head, swam for about a second, and then floated again (Russell 1976). Until the calf was three weeks old, it was not able to dive easily even in 3 m-deep water. This also helps to explain why cows do not feed very much when their calves are young. At three weeks, the calf could hold its breath for up to 4 minutes and could dive to the bottom of the pool (Russell 1976). Loughrey (1959) also observed that a calf in summer can hold its breath for up to 5 minutes.

The rapid development of the calf also was demonstrated in its

relative strength. Russell (1976) observed that the 3-week-old calf was able to climb out onto the haulout area by pushing off from the mother with its hind flippers. The cow was also observed to push the calf with her front flippers as it attempted to climb out (Russell 1976). By one month, the calf was able to climb onto the deck without assistance.

The suckling bouts that I observed at Marineland averaged 7 minutes in length (N=101). These bouts were less than half as long as those (17 minutes; N=5) of the wild calves on land that were observed by Salter (1978). However, the calves that Salter observed were several months older than the one that I observed, which may have had an influence on the duration of bouts. Also, because he did not state his criterion for defining the duration of a "bout", I cannot determine whether our results are comparable. For aquatic suckling Miller and Boness (1983) recorded an average suckling bout duration of 11.7 minutes for 25 bouts. Overall, the percentage of time spent suckling that I observed was relatively constant for the captive calf, the wild calves, and the wild juveniles (9 to 11%).

For the Marineland cow/calf pair that I observed in 1982, suckling bouts were initiated somewhat more often by the cow (56%) than by the calf (44%). Initiation of a suckling bout is very difficult to determine, and relies heavily on subtle movements and low volume vocalizations. The walrus calf that I observed initiated suckling by bellowing and rubbing the cow's side with its vibrissae.

Similar behaviors and functions have been described for other species of pinnipeds. Wilson (1974) observed that maternal stroking initiates suckling bouts in Phoca vitulina. Grey seal and northern elephant seal pups vocalize and nudge the female's side to initiate suckling (Fogden 1968, 1971; LeBoeuf et al. 1972). Due to the difficulty of observing these behaviors on crowded walrus haulouts, I was unable to obtain comparable data from wild walruses.

Termination of suckling bouts was somewhat easier to identify. My data from observations of the captive cow/calf pair showed that the calf terminated 69% of the suckling bouts, the female 27%, and the male 4% by interference (N=98). Salter (1978) reported that the females and calves that he observed terminated suckling bouts with equal frequency (36%), and that other walruses terminated the bouts by disturbing the pair with a frequency of 28% (N=14). Zabel et al. (1982) observed that the calves terminated 50% of the suckling bouts, the female 17%, and others 25% (N=12). Unfortunately, the sample sizes for both Salter's (1978) and Zabel et al.' s (1982) data were too small to be statistically meaningful in comparison. However, it appears as though their data are very similar but that both differ from my study with respect to the effects of disturbance caused by others.

Pederson (1962:24) reported that R. Muller observed in the fall of 1897 that the cow will protect her calf by attacking another animal that approaches the calf "too closely". McCullogh (1974:2) concluded

that female walruses with calves were the "most aggressive animals" on a haul-out site in Hudson Bay. My findings showed that while the male struck the female in 13% of agonistic encounters, the female struck the male in 17%. The reports of Salter (1978) and Zabel et al. (1982) indicated a higher degree of aggressive behavior in wild walruses. Salter (1978) found that males struck in 44% of agonistic encounters and females in 28%. Zabel et al. (1982) found that females without calves struck in approximately the same number of agonistic encounters as males (38% and 37%) while females with calves struck in 56% of agonistic encouners. Female walruses perform the same threat behaviors as males, but their threats are "more stylised and less severe" (Miller 1982:31), and the females do "not annoy and agitate each other in the manner of bulls" (Brooks 1954:64). It may be that female walruses often use the more subtle threat signals, at least in captivity.

Striking by the male, female, or both at Marineland took place in only 25% of the 164 agonistic encounters that I observed. This is a much lower value than was reported by Salter (1978) of 68% (N=43) or Zabel et al. (1982) of 43% (N=182).

As in the foregoing, this indicates that the Marineland animals had a much lower level of aggressive behavior than do the wild walruses. Because the captive animals live together all the time, they may develop a more harmonious relationship or more subtle ways to show annoyance. Since they are housed only as pairs, each in an enclosure

of its own, they are much less exposed to competitive contact with others than if they were in a large group in the wild.

Miller and Boness (1983) stated that wild dependent young interacted with walruses other than their mothers 6% of the time. The captive calf that I observed in 1982 spent only 1.4% of its time interacting with the adult male. This proportion might increase with age and probably with the number of other animals present.

During interactions with other animals, calves often were subjected to aggressive behaviors. Zabel et al. (1982) reported that wild calves received an average of 2.4 strikes/hour. Of the interactions that I observed between the captive calf and the male, the calf received an average of 0.16 strikes per hour (N=15), and 0.15 threats per hour (N=48). The female responded to 85% of those threats very quickly (mean = 4 sec). These responses included strikes (7%), kinesic tusk threats (7%), vocal threats (46%) and calling the calf (33%). Zabel et al. (1982) found that the female responded to the calf's being struck in only 29% of the instances (N=31), and the cow's responses were to strike (3%) or to threaten (26%). The low proportion of female responses in Zabel et al.'s (1982) data compared with mine could be partly due to the fact that Zabel et al. (1982) were observing the wild walruses in a large herd, from a position 50 to 100 meters away, and could not hear any but the loudest of vocal threats.

The frequency of tusk strikes has been used to assess the relative dominance of individuals (Miller 1975b, 1982; Salter 1978).

Strikes have been used because they are easy to observe from a long distance. Miller (1982) also has examined the use of kinesic tusk threats (KTT's) by females. He found that KTT's occurred in 40% of all agonistic encounters between females. I obtained similar results of agonistic encounters between the male and female; KTT's by the elder female occurred in 44% of all agonistic interactions.

Miller (1982) and Zabel et al. (1982) observed that females use KTT's more frequently than males do. Zabel et al. (1982) also observed that females often defended their young with KTT's. The female that I observed also used KTT's more than the male did, and the female responded not only by striking but by vocal threats or by calling the calf.

The Marineland calf also was observed to respond frequently to the vocalizations of the female by approaching her. Pup attraction calls are very important in several species of pinnipeds, including California sea lions (Peterson and Bartholomew 1967), northern elephant seals (Bartholomew and Collias 1962; Le Boeuf et al. 1972; Petrinovich 1974), and southern fur seals (Stirling and Warneke 1971). Although these vocalizations are not threats, they do serve to protect the young by maintaining proximity.

The Marineland calf whose birth I observed was active immediately after birth, but it appeared weak and did not orient toward the female or appear to respond to her movements or vocalizations. I found that the cow was responsible for maintaining proximity with the calf for

the first 2 days, and that it did so by approaching the calf when the calf withdrew. After two days, the calf was more responsive and approached more frequently. Christenson and Le Boeuf (1978) observed similar behavior in the northern elephant seal. They found that immediately after birth the pups' "movement patterns are poorly coordinated" (p. 169) and the pups were unable to respond to the females' pup attraction calls. For those reasons, Christenson and Le Boeuf (1978:169) suggested that the female's aggression "enhances reproductive success by increasing the chances that the young will survive."

Hinde (1974) also found that in rhesus monkeys, for the first few weeks after birth, the mother was responsible for maintaining proximity. Taber and Thomas (1982) found that right whale calves are more active than their mothers; they leave and approach the mother more frequently than she leaves or approaches them. Taber and Thomas (p. 1081) stated that the activity of the calves can be called "play", but that the relatively "few directed movements" by the mother are what they believe to be really significant. It is possible that vocalizations play an important role in the reunion of the mother and calf right whale, in much the same manner as they do for walruses.

The role of vocalizations between the cow and calf walrus when they are separated has been described by several investigators (Heinrich 1947; Nikulin 1941; Bel'kovich and Yablokov 1961; Miller and Boness 1983). The young bellow repeatedly when they are troubled

(Miller and Boness 1983; Loughrey 1959). In large groups, vocalizations appear to be important as a means of communication. The soft vocalizations can be heard only at close range.

At Marineland, I found that the cow used vocalizations to initiate suckling bouts, to reassure the calf of her presence, and to call the calf to her. The calf vocalized when in danger, and when attempting to initiate a suckling bout. Christenson and Le Boeuf (1978) observed that the responsiveness of the female northern elephant seal to its pup's vocalization for initiation of a suckling bout affected the pup's chances of survival. Sandegren (1970) pointed out the importance of vocalization for mutual recognition in Steller sea lions after the first week to 10 days of life. These vocalizations are of importance in reuniting females with their pups when they had been separated.

This study of the reproductive behavior of captive walruses shows that in many ways captive walruses are physiologically and behaviorally similar to wild walruses. The study of captive walrus behavior therefore, provides insights into some of the questions that are virtually impossible to examine in the wild. The results presented in this thesis suggest possible answers to those questions and provide a basis for further examination of walrus behavior. Behaviors that should be examined more intensely in the wild include the courtship displays of adult male walruses and the role of vocalizations of the wild cow and calf with respect to the changes in

their relationship during the early months of the calf's life. Physiological studies of wild walruses could determine whether the energy consumption pattern of captive walruses is analagous to that of wild animals.

SUMMARY

Pacific walruses (Odobenus rosmarus divergens) spend most of their life in association with the pack ice. They winter in ice-covered areas of the Bering Sea, where they breed. In the spring as the ice melts and breaks up, the females, young, and a few adult males migrate northward. Along the way, calving takes place, mainly in May. These walruses then spend the summer in the edge of the pack ice in the Chukchi Sea, while most of the adult males remain in the Bering Sea throughout the summer. In the summer, in all of those areas, walruses complete their molt, shedding and renewing their pelage. In the autumn, when the ice forms southward, the females and young swim southward again to the Bering Sea, where they are rejoined by the males for the breeding season.

Because walruses under natural conditions are far from shore in ice-covered arctic waters throughout most of the year, the study of their behavior is difficult and has been somewhat retarded. Wild walruses tend to haul out in large groups and to return to the water periodically to feed. For those reasons, continual observation of the same individuals for even a few days at a time usually is not feasible in the wild, but it is feasible in oceanaria.

I conducted behavioral observations of two pairs of breeding adult walruses in captivity at Marineland in California and analyzed existing records of their food intake to obtain seasonal comparisons and for comparison with existing data from wild walruses. The

behavioral aspect of this study examined the breeding behavior including courtship displays, male/female interactions, and cow/calf behavior. Some information on cow/calf behavior of wild walruses also was obtained in the Chukchi Sea for comparison.

The Marineland walruses consumed increasing amounts of food as they grew older and larger, but the amount consumed per unit of body weight decreased with increasing age. The gross energy intake per day for males tended to be about 40% greater than for females at the same age, but the relative intakes were about the same for both sexes, when the females were not pregnant or lactating.

Adult males consumed fewer kcal/day during the breeding season than at other times of the year. Following that period, their intake increased steadily to the following December. The adult females fasted briefly during the breeding season, apparently at the time of estrus. The females consumed 40 - 50% more energy during pregnancy than when not pregnant or lactating; their consumption increased about 50% during lactation.

The captive male walruses performed courtship display behaviors throughout the year. Nonetheless, they spent more time displaying, performed more displays per hour, and their displays were performed in a more stereotyped manner during the breeding season. The intensity with which the two captive males displayed, and the responses of each to the displays of the other, whom they could only hear and not see, indicated that the tendency to display is innate and very strong.

During the breeding season, interactions between the male and female generally were initiated by the female. At other times, the male most often initiated the interactions and the female terminated them. Male/female interactions took place more frequently, were longer in duration, and more often resulted in mounting outside than inside the breeding season. Courtship displays were followed by male/female interactions more often outside than during the the breeding season. However, more interactions were preceded by displays during the breeding season than at other times.

The female at Marineland was responsible for maintaining proximity with the calf for the first two days after birth. After two days, the calf was more alert and agile and was observed to respond frequently to the vocalizations of the female by approaching her. The female used vocalizations to initiate suckling bouts, to reassure the calf of her presence, and to call the calf to her. The calf vocalized when in danger, and when attempting to initiate a suckling bout.

The calf began suckling within 6.5 hours after birth. The average duration of a suckling bout was about 7 minutes. Both the captive and the wild calves and juveniles spent from 9 to 11% of the daylight hours in suckling.

The captive calf spent 1.4% of its time interacting with the adult male. During those interactions, the calf was threatened by the male 0.51 times per hour, but the male struck the calf an average of only 0.16 times per hour. The female responded to the male's threats

to the calf very quickly with either a tusk strike, a kinesic tusk threat, a vocal threat, or by calling the calf.

Appendix I. Mean daily consumption of energy per calendar year (January - December) for the walruses at Marineland in relation to estimated body weight.

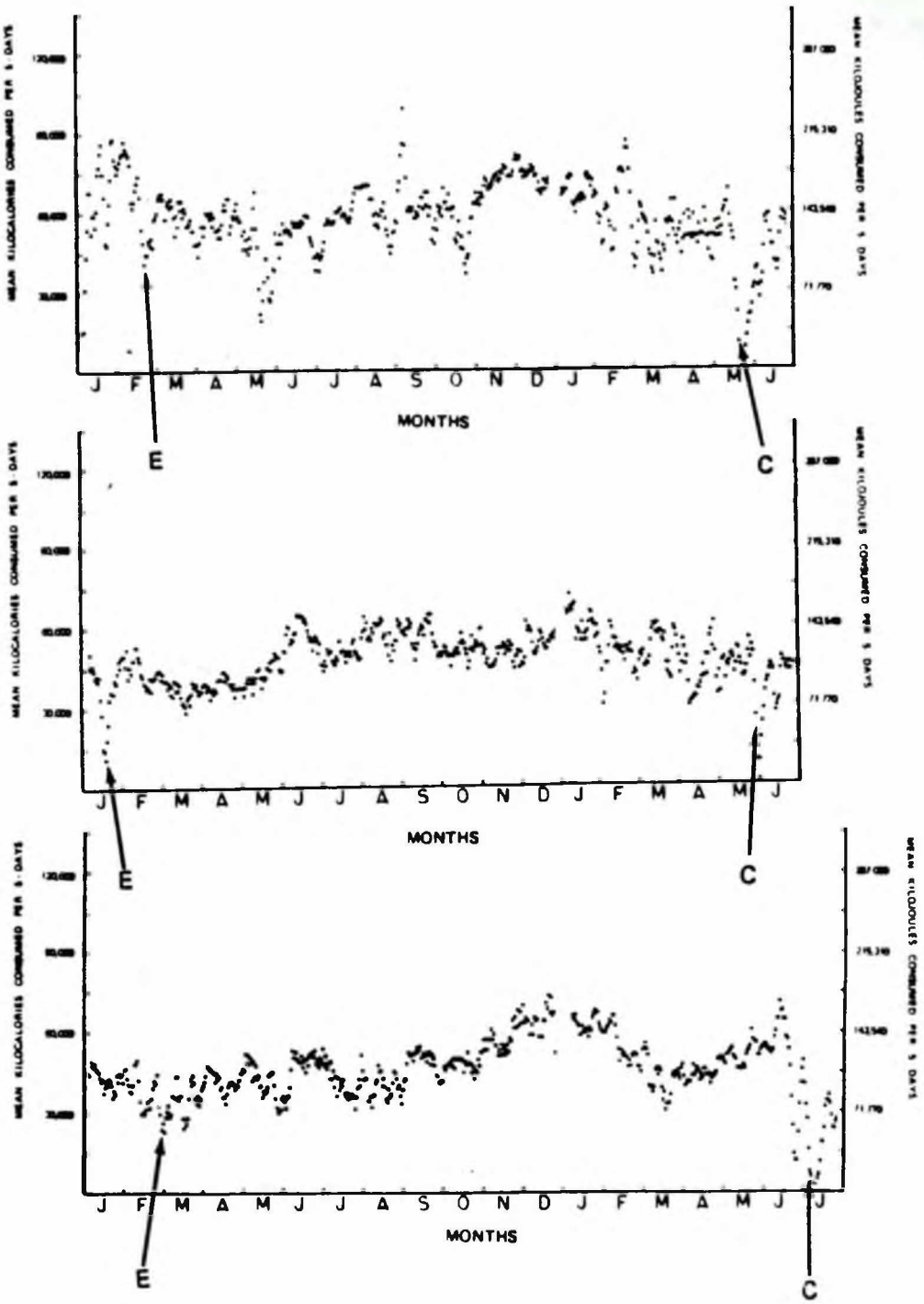
Sex	Age (yrs.)	Estimated TBW (kg)	Mean daily intake	
			kcal	kcal/kg$^{3/4}$TBW
Male	2	300	25,554	354
	3	400	27.591	308
	4	500	32,615	308
	7	650	41.291	321
	8	700	37,521	276
	9	725	36,036	258
	10	775	38,452	262
	11	825	41,502	270
	12	875	51,121	318
	13	950	44,705	261
	14	1050	41.355	224
			51,161	277
	15	1125	49,896	257
			56.755	292
	16	1175	46.804	233
	17	1200	51,860	254
	18	1200	70,307	345
	19	1200	55,702	273
	20	1200	55,136	270
	21	1200	50,175	246

Appendix I. (continued).

Sex	Age (yrs.)	Estimated TBW (kg)	Mean daily intake	
			kcal	kcal/kg$^{3/4}$TBW
Female (nonpregnant nonlactating)	2	200	25,119	472
	3	300	27,529	382
	4	350	32,024	396
	7	575	43.011	366
	8	650	40,995	318
	9	700	33,685	248
	19	830	36,834	238
Female (pregnant and/or lactating)	10	750	44,682	312
	11	800	41,125	320
	12	830	58,281	377
	13	830	56.330 45,555	364 295
	14	830	54,035	349
	15	830	53,937	349
	16	830	46.809	303
	17	830	54,444	352
	18	830	50,414	326
	20	830	48,305	312

APPENDIX II

Five point running averages of daily energy consumption during two pregnancies for the older (upper) and one pregnancy for the younger (lower) of the two female walruses at Marineland.


MEAN KILOCALORIES CONSUMED PER 5 DAYS
MEAN KILOJOULES CONSUMED PER 5 DAYS
J F M A M J J A S O N D J F M A M J
MONTHS
E
C

APPENDIX III

Five point running averages of daily energy consumption for the younger male walrus in nine different years (Figures 26, 27, and 28) and for the older male walrus in eight different years (Figures 29, 30, and 31).

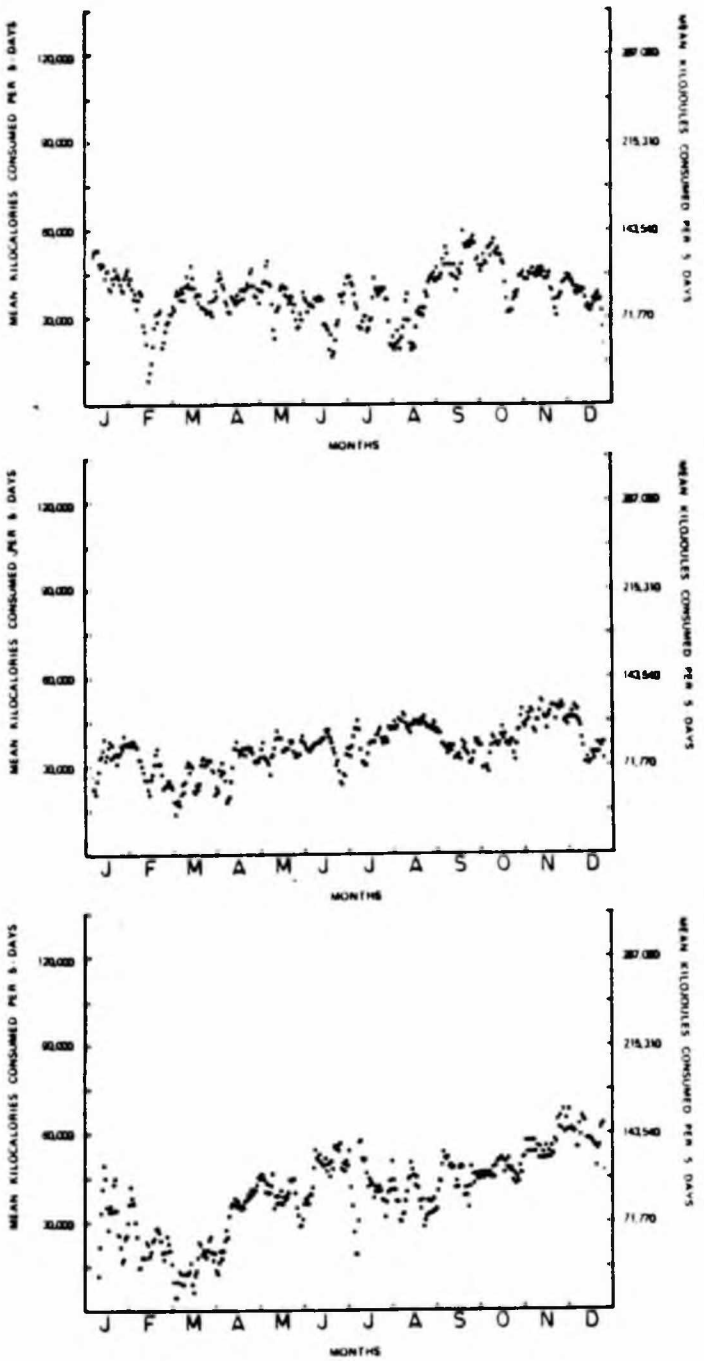


Figure 26. Five point running averages of daily energy consumption for the younger male walrus at 8, 9, and 10 years of age at Marineland.

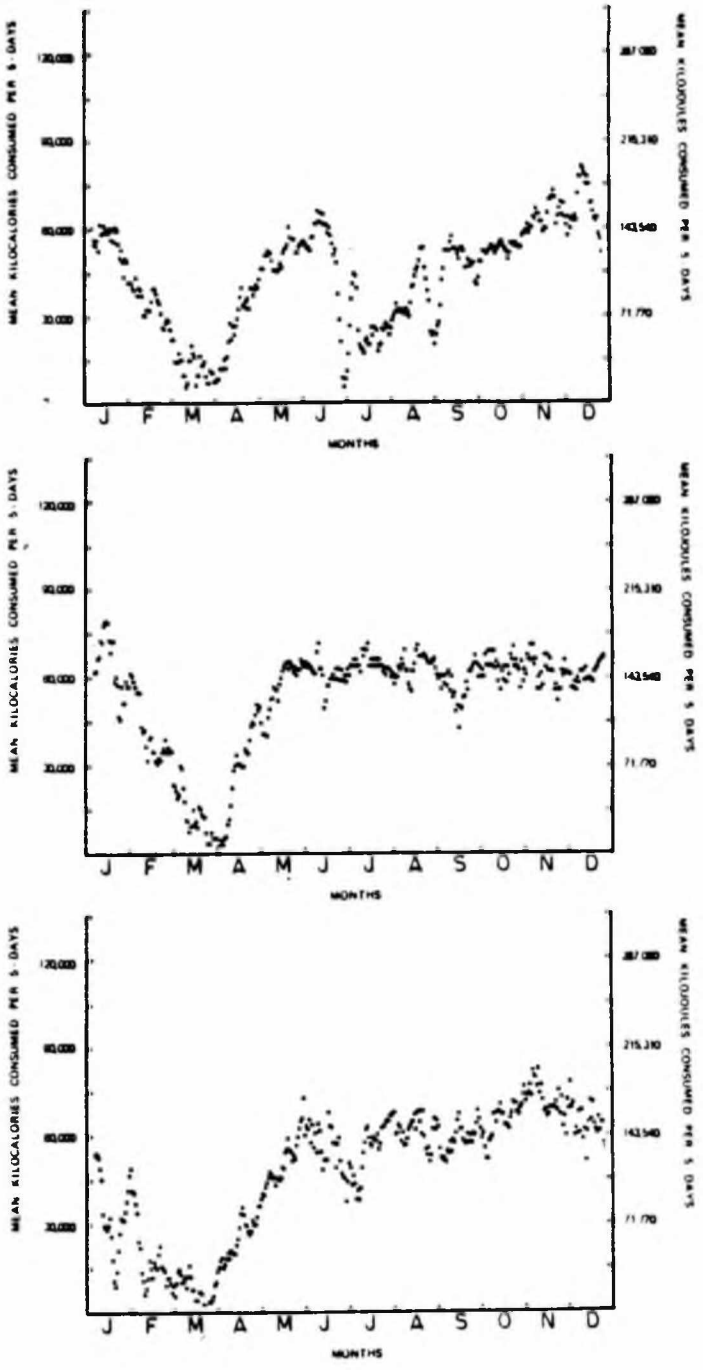


Figure 27. Five point running averages of daily energy consumption for the younger male walrus at 11, 12, and 13 years of age at Marineland.

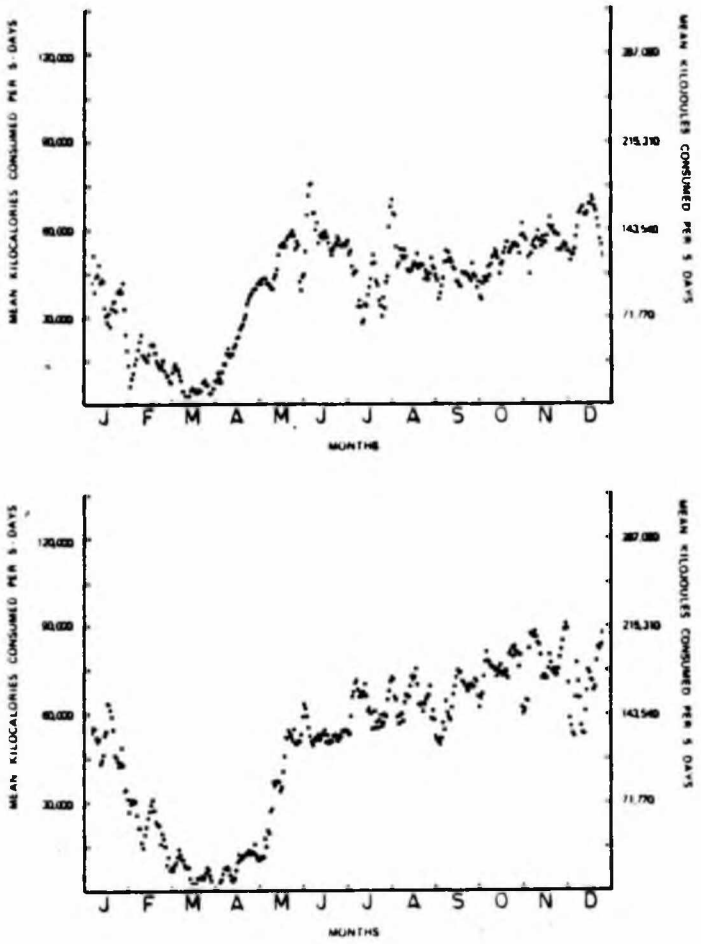


Figure 28. Five point running averages of daily energy consumption for the younger male walrus at 14 and 15 years of age at Marineland.

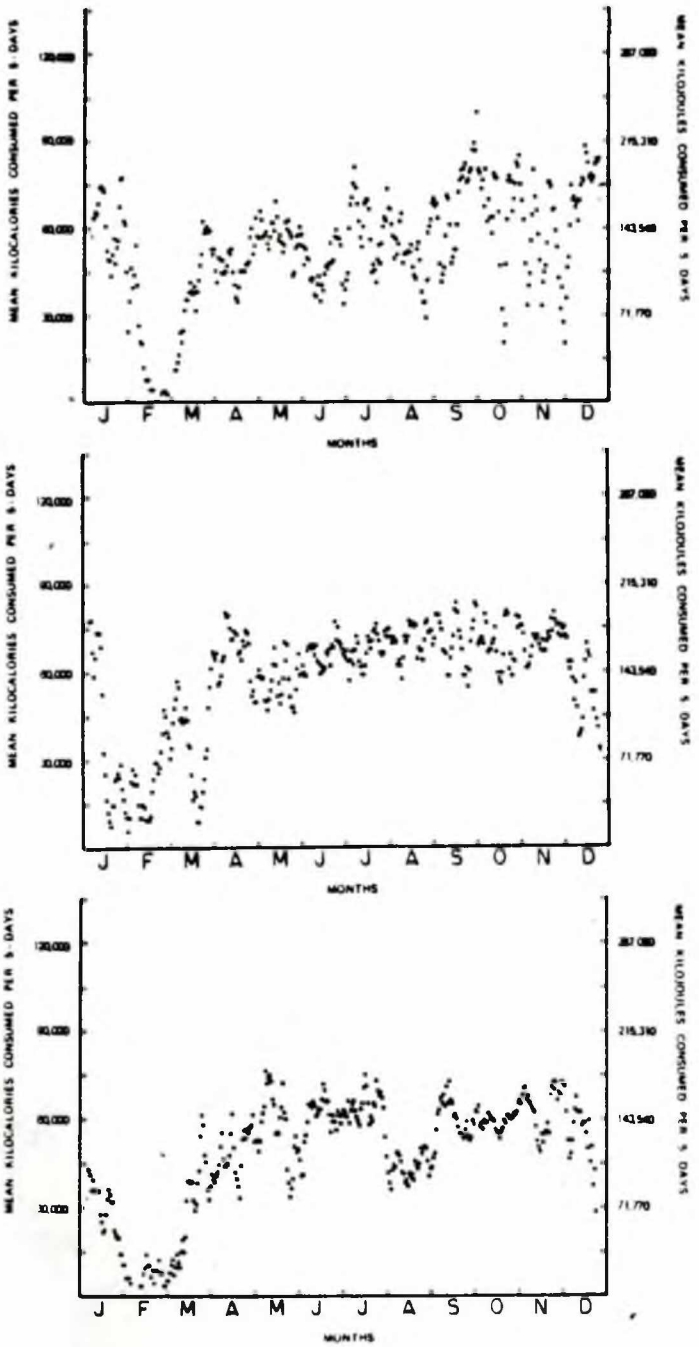


Figure 29. Five point running averages of daily energy consumption for the older male walrus at 14, 15, and 16 years of age at Marineland.

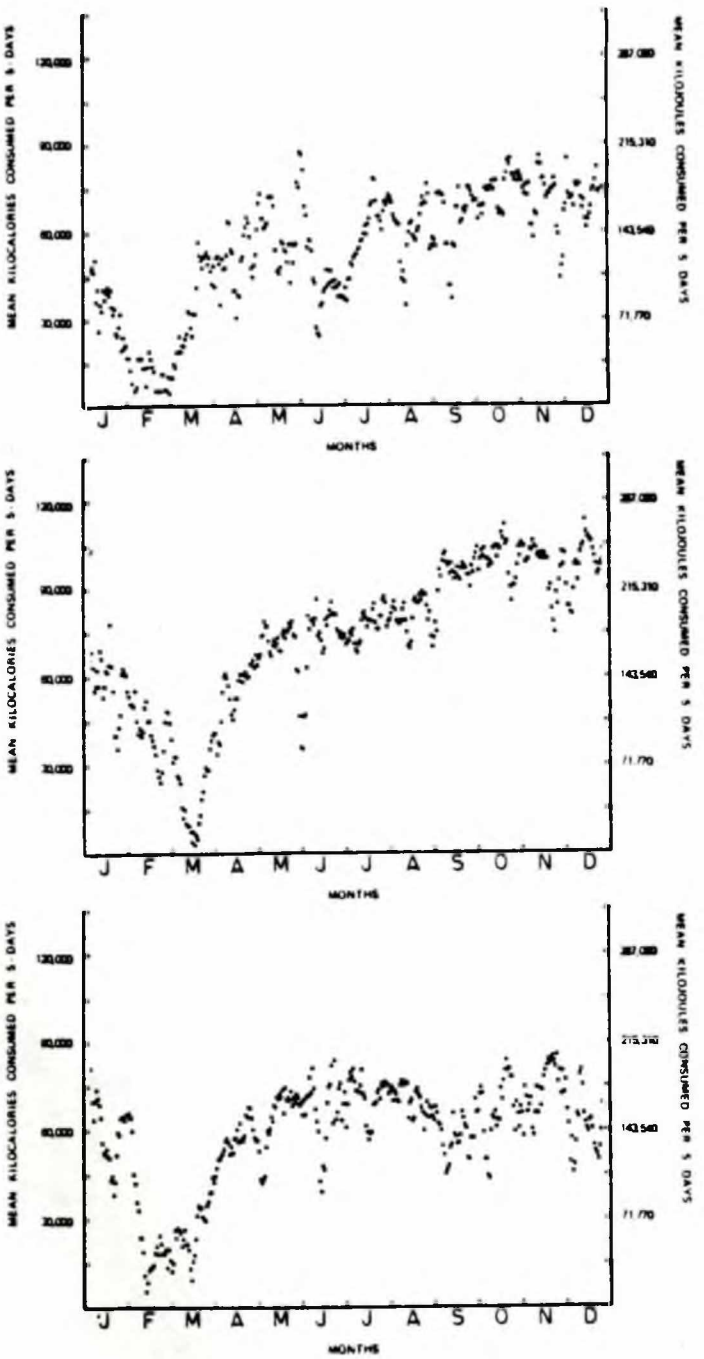


Figure 30. Five point running averages of daily energy consumption for the older male walrus at 17, 18, and 19 years of age at Marineland.

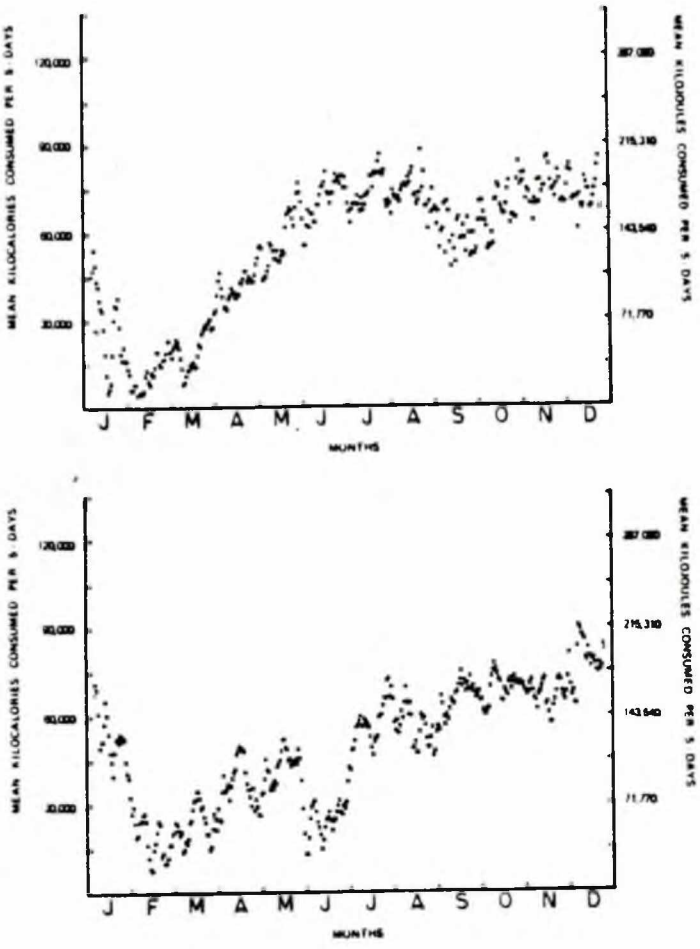


Figure 31. Five point running average of daily energy consumption for the older male walrus at 20 and 21 years of age at Marineland.

APPENDIX IV

The transition frequency matrices for the two adult male walruses at Marineland from observations made outside the breeding season (Table 11). The behaviors for the younger male are as follows: 1=surface, 2=up, 3=float, 4=sink, 5=splash, 6=whistle, 7=swim around, 8=splutter, 9=bubble, 10=groan, 11=bark. The behaviors for the older male are as follows: 1=dive, 2=float, 3=rest, 4=splash, 5=whistle, 6=swim around, 7=splutter, 8=bubble, 9=groan, 10=bark.

The transition frequency matrices for the two adult male walruses at Marineland from observations made during the breeding season from above the water surface (Table 12). The behaviors for the younger male are as follows: 1=surface, 2=up, 3=dive, 4=float, 5=sink, 6=splash, 7=whistle, 8=swim around, 9=pulses in the air, 10=splutter, 11=bubble, 12=groan, 13=bark. The behaviors for the older male are as follows: 1=surface, 2=up, 3=rest, 4=dive, 5=float, 6=sink, 7=splash, 8=whistle, 9=swim around, 10=pulses in the air, 11=splutter.

The transition frequency matrices for the two adult male walruses at Marineland from observations made during the breeding season from below the water surface (Table 13). The behaviors for the younger male are as follows: 1=surface, 2=up, 3=dive, 4=float, 5=sink, 6=splash, 7=bell, 8=whistle, 9=whine, 10=pulses underwater. The behaviors for the older male are as follows: 1=surface, 2=up, 3=rest, 4=dive, 5=float, 6=sink, 7=splash, 8=whistle, 9=whine, 10=pulses

Table 11. The transition frequency matrices for the younger (upper), and the older (lower) of the two adult male walruses at Marineland from observations made outside the breeding season.

		SECOND BEHAVIOR										
		1	2	3	4	5	6	7	8	9	10	11
FIRST BEHAVIOR	1	0	1	1	4	0	0	0	2	0	0	0
	2	5	0	4	1	67	75	10	6	4	0	11
	3	0	11	0	0	8	3	1	7	3	0	1
	4	0	5	2	0	2	4	0	1	0	0	3
	5	1	155	6	10	0	17	3	37	9	0	13
	6	0	35	5	4	33	0	4	18	8	0	24
	7	0	5	1	0	11	3	0	2	3	0	2
	8	0	6	6	6	42	7	6	0	8	0	31
	9	0	6	0	0	15	2	1	8	0	1	8
	10	0	0	0	0	0	1	0	1	0	0	3
	11	0	11	0	1	11	12	3	22	4	2	0

		SECOND BEHAVIOR									
		1	2	3	4	5	6	7	8	9	10
FIRST BEHAVIOR	1	0	1	2	16	9	5	12	3	0	1
	2	2	0	2	3	10	0	3	2	0	1
	3	2	2	0	4	6	0	12	4	0	2
	4	26	6	17	0	10	0	19	3	0	2
	5	3	3	2	18	0	1	55	13	3	12
	6	2	1	0	4	2	0	1	1	0	0
	7	9	2	8	26	57	2	0	9	3	10
	8	2	1	5	4	19	1	13	0	0	1
	9	0	0	0	0	2	0	2	1	0	1
	10	3	1	1	4	11	0	8	0	1	0

Table 12. The transition frequency matrices for the younger (upper) and older (lower) of the two adult males walruses at Marineland, from observations made from above the water surface during the breeding season.

SECOND BEHAVIOR

FIRST BEHAVIOR	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	6	5	56	0	0	0	0	0	1	0	0	0
2	0	0	37	63	642	141	175	0	29	5	0	2	3
3	7	267	0	42	0	1	0	4	3	1	0	0	0
4	2	123	199	0	13	8	2	4	1	0	2	0	0
5	53	433	29	100	0	2	4	1	88	2	4	1	0
6	0	1	118	23	2	0	0	0	3	2	0	1	2
7	1	76	5	21	65	1	0	0	5	3	1	1	1
8	0	2	2	3	0	0	0	0	1	0	0	0	0
9	0	6	13	94	10	1	3	0	0	1	0	2	2
10	0	4	2	3	3	1	3	0	3	0	0	0	2
11	1	3	5	1	0	1	0	0	0	0	0	0	0
12	0	1	1	1	1	0	1	0	0	3	0	0	0
13	0	2	0	2	2	0	0	0	1	0	0	1	0

SECOND BEHAVIOR

FIRST BEHAVIOR	1	2	3	4	5	6	7	8	9	10	11
1	0	81	316	1	8	0	0	0	0	0	0
2	3	0	1	216	4	17	1	1	2	8	5
3	0	74	0	10	142	0	2	1	1	0	2
4	264	5	10	0	1	0	0	0	0	1	0
5	4	29	10	50	0	9	0	5	1	2	1
6	5	6	8	1	3	0	0	0	1	0	0
7	0	0	0	2	1	0	0	0	0	1	0
8	0	0	0	0	2	0	0	0	0	2	4
9	0	2	1	0	1	0	0	0	0	0	0
10	1	0	0	3	1	0	1	0	0	0	2
11	0	0	0	0	0	0	0	2	0	3	0

Table 13. The transition frequency matrices for the younger (upper) and older (lower) of the two adult males walruses at Marineland. from observations made from below the water surface through the window during the breeding season.

		SECOND BEHAVIOR										
		1	2	3	4	5	6	7	8	9	10	11
F												
I	1	0	7	1	85	0	0	0	0	0	0	0
R	2	0	0	143	269	696	177	0	88	2	5	3
S	3	0	267	0	47	10	9	0	1	10	16	16
T	4	4	311	57	0	5	11	2	1	13	100	18
	5	0	108	3	4	0	0	464	30	10	105	1
B	6	0	1	167	15	0	0	0	0	0	0	1
E	7	98	279	5	66	0	0	0	3	0	1	0
H	8	0	87	7	21	9	0	0	0	3	3	0
A	9	0	39	3	13	0	1	0	11	0	24	1
V	10	1	151	5	5	4	0	3	1	59	0	3
I	11	0	17	5	17	2	0	0	0	1	0	0
O												
R												

	SECOND BEHAVIOR													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
F1	0	156	426	12	40	1	0	0	0	5	0	0	0	0
I2	6	0	4	274	17	5	5	0	0	0	0	23	6	10
R3	8	66	0	8	286	0	1	0	19	2	0	11	1	0
S4	373	8	23	0	10	0	1	0	7	24	0	35	0	2
T5	69	55	31	138	0	3	2	2	10	47	0	4	7	0
6	0	1	3	1	2	0	0	1	0	0	0	0	7	0
B7	1	0	0	4	4	0	0	0	0	0	0	0	0	1
E8	0	0	0	0	2	0	2	0	0	3	0	0	0	0
H9	2	20	8	12	56	0	0	0	0	4	0	3	3	0
A10	20	6	8	19	1	0	1	0	13	0	0	18	1	0
V11	0	0	2	9	9	1	0	0	69	2	1	0	0	0
I12	0	2	0	2	3	0	0	0	0	4	0	1	0	1
013	0	3	0	1	2	0	1	4	0	0	0	1	1	0
R14	0	0	0	0	0	0	0	0	0	0	0	0	0	0

underwater, 11=hit wall with front flipper, 12=pulses in the air. 13=splutter.

APPENDIX V

The transition probability matrices for the two adult male walruses at Marineland from observations made outside the breeding season (Table 14). The behaviors for the younger male are as follows: 1=surface, 2=up, 3=float, 4=sink, 5=splash, 6=whistle, 7=swim around, 8=splutter, 9=bubble, 10=groan, 11=bark. The behaviors for the older male are as follows: 1=dive, 2=float, 3=rest, 4=splash, 5=whistle, 6=swim around, 7=splutter, 8=bubble, 9=groan, 10=bark.

The transition probability matrices for the two adult male walruses at Marineland from observations made during the breeding season from above the water surface (Table 15). The behaviors for the younger male are as follows: 1=surface, 2=up, 3=dive, 4=float, 5=sink, 6=splash, 7=whistle, 8=swim, 9=pulses in the air, 10=splutter, 11=bubble, 12=groan, 13=bark. The behaviors for the older male are as follows: 1=surface, 2=up, 3=rest, 4=dive, 5=float, 6=sink, 7=splash, 8=whistle, 9=swim around, 10=pulses in the air. 11=splutter.

The transition probability matrices for the two adult male walruses at Marineland from observations made during the breeding season from below the water surface (Table 16). The behaviors for the younger male are as follows: 1=surface, 2=up, 3=dive, 4=float, 5=sink, 6=splash, 7=bell, 8=whistle, 9=whine, 10=pulses underwater. The behaviors for the older male are as follows: 1=surface, 2=up, 3=rest, 4=dive, 5=float, 6=sink, 7=splash, 8=whistle, 9=whine,

Table 14. The transition probability matrices for the younger (upper) and the older (lower) of the two male walruses at Marineland from observations made outside the breeding season.

FIRST BEHAVIOR	SECOND BEHAVIOR 1	2	3	4	5	6	7	8	9	10	11
1	0.0000	0.1250	0.1250	0.5000	0.0000	0.0000	0.0000	0.2500	0.0000	0.0000	0.0000
2	0.0273	0.0000	0.0219	0.0055	0.3661	0.4098	0.0546	0.0328	0.0219	0.0000	0.0601
3	0.0000	0.3235	0.0000	0.0000	0.2353	0.0882	0.0294	0.2059	0.0882	0.0000	0.0294
4	0.0000	0.2941	0.1176	0.0000	0.1176	0.2353	0.0000	0.0588	0.0000	0.0000	0.1765
5	0.0040	0.6175	0.0239	0.0398	0.0000	0.0677	0.0120	0.1474	0.0359	0.0000	0.0518
6	0.0000	0.2672	0.0382	0.0305	0.2519	0.0000	0.0305	0.1374	0.0611	0.0000	0.1832
7	0.0000	0.1852	0.0370	0.0000	0.4074	0.1111	0.0000	0.0741	0.1111	0.0000	0.0741
8	0.0000	0.0536	0.0536	0.0536	0.3750	0.0625	0.0536	0.0000	0.0714	0.0000	0.2768
9	0.0000	0.1463	0.0000	0.0000	0.3659	0.0488	0.0244	0.1951	0.0000	0.0244	0.1951
10	0.0000	0.0000	0.0000	0.0000	0.0000	0.2000	0.0000	0.2000	0.0000	0.0000	0.6000
11	0.0000	0.1667	0.0000	0.0152	0.1667	0.1818	0.0455	0.3333	0.0606	0.0303	0.0000

FIRST BEHAVIOR	SECOND BEHAVIOR 1	2	3	4	5	6	7	8	9	10
1	0.0000	0.0204	0.0408	0.3265	0.1837	0.1020	0.2449	0.0612	0.0000	0.0204
2	0.0870	0.0000	0.0870	0.1304	0.4348	0.0000	0.1304	0.0870	0.0000	0.0435
3	0.0625	0.0625	0.0000	0.1250	0.1875	0.0000	0.3750	0.1250	0.0000	0.0625
4	0.3133	0.0723	0.2048	0.0000	0.1205	0.0000	0.2289	0.0361	0.0000	0.0241
5	0.0273	0.0273	0.0182	0.1636	0.0000	0.0091	0.5000	0.1182	0.0273	0.1091
6	0.1818	0.0909	0.0000	0.3636	0.1818	0.0000	0.0909	0.0909	0.0000	0.0000
7	0.0714	0.0159	0.0635	0.2063	0.4524	0.0159	0.0000	0.0714	0.0238	0.0794
8	0.0435	0.0217	0.1087	0.0870	0.4130	0.0217	0.2826	0.0000	0.0000	0.0217
9	0.0000	0.0000	0.0000	0.0000	0.3333	0.0000	0.3333	0.1667	0.0000	0.1667
10	0.1034	0.0345	0.0345	0.1379	0.3793	0.0000	0.2759	0.0000	0.0345	0.0000

Table 15. The transition probability matrices for the youngest (upper) and the older (lower) of the two adult male walruses at Marinaland from observations made during the breeding season from above the water surface.

FIRST BEHAVIOR	SECOND BEHAVIOR												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0.0000	0.0882	0.0735	0.8235	0.0000	0.0000	0.0000	0.0000	0.0000	0.0147	0.0000	0.0000	0.0000
2	0.0000	0.0000	0.0377	0.0574	0.5852	0.1285	0.1595	0.0000	0.0266	0.0046	0.0000	0.0018	0.0027
3	0.0215	0.8215	0.0000	0.1282	0.0000	0.0031	0.0000	0.0123	0.0092	0.0031	0.0000	0.0000	0.0000
4	0.0057	0.3473	0.5621	0.0000	0.0367	0.0266	0.0057	0.0113	0.0028	0.0000	0.0057	0.0000	0.0000
5	0.0739	0.6039	0.0406	0.1395	0.0000	0.0028	0.0056	0.0014	0.1227	0.0028	0.0056	0.0014	0.0028
6	0.0000	0.0044	0.7763	0.1513	0.0132	0.0000	0.0000	0.0000	0.0197	0.0132	0.0000	0.0044	0.0132
7	0.0056	0.4222	0.0278	0.1167	0.3611	0.0056	0.0000	0.0000	0.0278	0.0167	0.0056	0.0056	0.0056
8	0.0000	0.2500	0.2500	0.3750	0.0000	0.0000	0.0000	0.0000	0.1250	0.0000	0.0000	0.0000	0.0000
9	0.0000	0.0459	0.0985	0.7121	0.0758	0.0076	0.0227	0.0000	0.0000	0.0076	0.0000	0.0152	0.0152
10	0.0000	0.1905	0.0952	0.1428	0.1429	0.0476	0.1428	0.0000	0.1429	0.0000	0.0000	0.0000	0.0952
11	0.0909	0.2727	0.4545	0.0909	0.0000	0.0909	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
12	0.0000	0.1250	0.1250	0.1250	0.1250	0.0000	0.1250	0.0000	0.0000	0.3750	0.0000	0.0000	0.0000
13	0.0000	0.2500	0.0000	0.2500	0.2500	0.0000	0.0000	0.0000	0.1250	0.0000	0.0000	0.1250	0.0000

FIRST BEHAVIOR	SECOND BEHAVIOR										
	1	2	3	4	5	6	7	8	9	10	11
1	0.0000	0.1995	0.7783	0.0025	0.0107	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
2	0.0116	0.0000	0.0030	0.8372	0.0155	0.0659	0.0039	0.0039	0.0078	0.0310	0.0194
3	0.0000	0.3190	0.0000	0.0431	0.6121	0.0000	0.0086	0.0043	0.0043	0.0000	0.0086
4	0.9393	0.0178	0.0356	0.0000	0.0030	0.0000	0.0000	0.0000	0.0000	0.0030	0.0000
5	0.0360	0.2613	0.0901	0.6505	0.0000	0.0811	0.0000	0.0450	0.0090	0.0180	0.0090
6	0.2083	0.2500	0.3333	0.0417	0.1250	0.0000	0.0000	0.0000	0.0417	0.0000	0.0000
7	0.0000	0.0000	0.0000	0.5000	0.2500	0.0000	0.0000	0.0000	0.0000	0.2500	0.0000
8	0.0000	0.0000	0.0000	0.0000	0.2500	0.0000	0.0000	0.0000	0.0000	0.2500	0.5000
9	0.0000	0.5000	0.2500	0.0000	0.2500	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
10	0.1250	0.0000	0.0000	0.3750	0.1250	0.0000	0.1250	0.0000	0.0000	0.0000	0.2500
11	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.4000	0.0000	0.4000	0.0000

10=pules under water, 11=hit wall with front flipper, 12=pulses in the air, 13=splutter.

APPENDIX VI

The long run steady-state matrices for the two adult male walruses att Marineland from observations made outside the breeding season (Table 17). The behaviors for the younger male are as follows: 1=surface, 2=up, 3=float, 4=sink, 5=splash, 6=whistle, 7=swim around, 8=splutter, 9=bubble, 10=groan, 11=bark. The behaviors for the older male are as follows: 1=dive, 2=float, 3=rest, 4=splash, 5=whistle, 6=swim around, 7=splutter, 8=bubble, 9=groan, 10=bark.

The long run steady-state matrices for the two adult male walruses at Marineland from observations made during the breeding season from above the water surface (Table 18). The behaviors for the younger male are as follows: 1=surface, 2=up. 3=dive, 4=float, 5=sink, 6=splutter, 7=whistle, 8=swim around. 9=pulses in the air, 10=splutter, 11=bubble, 12=groan, 13=bark. The behaviors for the older male are as follows: 1=surface, 2=up, 3=rest, 4=dive, 5=float, 6=sink, 7=splash, 8=whistle, 9=swim around, 10=pulses in the air. 11=splutter.

The long run steady-state matrices for the two adult male walruses at Marineland from observations made during the breeding season from below the water surface (Table 19). The behaviors for the younger male are as follows: 1=surface, 2=up. 3=dive, 4=sink, 6=splash, 7=bell, 8=whistle, 9=whine, 10=pulses underwater. The behaviors for the older male are as follows: 1=surface, 2=up, 3=rest,

Table 17. The long run steady-state matrices for the younger (upper) and the older (lower) of the two adult male walruses at Marineland from observations made outside the breeding season.

FIRST BEHAVIOR	SECOND BEHAVIOR										
	1	2	3	4	5	6	7	8	9	10	11
1	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078
2	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078
3	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078
4	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078
5	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078
6	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078
7	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078
8	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078
9	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078
10	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078
11	0.0075	0.2393	0.0285	0.0271	0.2302	0.1565	0.0339	0.1206	0.0445	0.0043	0.1078

FIRST BEHAVIOR	SECOND BEHAVIOR									
	1	2	3	4	5	6	7	8	9	10
1	0.0924	0.0338	0.0684	0.1543	0.2368	0.0171	0.2500	0.0725	0.0165	0.0610
2	0.0924	0.0338	0.0684	0.1543	0.2368	0.0171	0.2500	0.0725	0.0165	0.0610
3	0.0924	0.0338	0.0684	0.1543	0.2368	0.0171	0.2500	0.0725	0.0165	0.0610
4	0.0924	0.0338	0.0684	0.1543	0.2368	0.0171	0.2500	0.0725	0.0165	0.0610
5	0.0924	0.0338	0.0684	0.1543	0.2368	0.0171	0.2500	0.0725	0.0165	0.0610
6	0.0924	0.0338	0.0684	0.1543	0.2368	0.0171	0.2500	0.0725	0.0165	0.0610
7	0.0924	0.0338	0.0684	0.1543	0.2368	0.0171	0.2500	0.0725	0.0165	0.0610
8	0.0924	0.0338	0.0684	0.1543	0.2368	0.0171	0.2500	0.0725	0.0165	0.0610
9	0.0924	0.0338	0.0684	0.1543	0.2368	0.0171	0.2500	0.0725	0.0165	0.0610
10	0.0924	0.0338	0.0684	0.1543	0.2368	0.0171	0.2500	0.0725	0.0165	0.0610

Table 18. The long run steady-state matrices for the younger (upper) and the older (lower) of the two adult male walruses at Marineland, from observations made during the breeding season from above the water surface.

FIRST BEHAVIOR \ SECOND BEHAVIOR	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
2	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
3	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
4	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
5	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
6	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
7	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
8	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
9	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
10	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
11	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
12	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030
13	0.0206	0.3255	0.1401	0.1312	0.2212	0.0470	0.0560	0.0035	0.0415	0.0056	0.0023	0.0025	0.0030

FIRST BEHAVIOR \ SECOND BEHAVIOR	1	2	3	4	5	6	7	8	9	10	11
1	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200
2	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200
3	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200
4	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200
5	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200
6	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200
7	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200
8	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200
9	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200
10	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200
11	0.2128	0.1517	0.1943	0.2113	0.1383	0.0212	0.0056	0.0157	0.0041	0.0252	0.0200

Table 10. The long run steady-state matrices for the younger (upper) and the older (lower) of the two adult male walruses at Marineland, from observations made during the breeding season through the underwater windows.

FIRST BEHAVIOR	SECOND BEHAVIOR 1	2	3	4	5	6	7	8	9	10	11
1	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066
2	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066
3	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066
4	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066
5	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066
6	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066
7	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066
8	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066
9	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066
10	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066
11	0.0266	0.3126	0.0962	0.1281	0.1667	0.0453	0.1067	0.0312	0.0250	0.0612	0.0066

FIRST BEHAVIOR	SECOND BEHAVIOR 1	2	3	4	5	6	7	8	9	10	11	12	13
1	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
2	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
3	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
4	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
5	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
6	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
7	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
8	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
9	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
10	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
11	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
12	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062
13	0.1946	0.1192	0.1643	0.1885	0.1758	0.0039	0.0053	0.0033	0.0506	0.0409	0.0389	0.0086	0.0062

4=dive, 5=float, 6=sink, 7=splash, 8=whistle, 9=whine, 10=pulses underwater, 11=hit wall with front flipper, 12=pulses in the air, 13=splutter.

Appendix VII. The calculations for the probability and standard error of the five-behavior sequence with the highest probability of occurrence for the older adult male walrus during the breeding season.

Using the values in the transition probability matrix (Table 16), the probabilities for transitions between behaviors 2 (up) and 4 (dive), 4 (dive) and 1 (surface), 1 (surface) and 3 (rest), 3 (rest) and 5 (float), and finally 5 (float) and 2 (up) were multiplied together to determine the probability of the sequence "up-dive-surface-rest-float-up".

$$\underset{\#2\text{-}4}{(0.8372)}\underset{\#4\text{-}1}{(0.9395)}\underset{\#1\text{-}3}{(0.7783)}\underset{\#3\text{-}5}{(0.6121)}\underset{\#5\text{-}2}{(0.2613)} = 0.0979$$

Now using the probability of the sequence (0.0979), the transition probabilities that were used in the above equation, and the total number of times that the first behavior in each of the transitions was observed (the sum of the rows in Table 13), the variance of this probability can be calculated.

$$\text{Variance} = (0.0979)^2 \left[\frac{1-0.8372}{(0.8372)(258)} + \frac{1-0.9395}{(0.9395)(281)} + \frac{1-0.7783}{(0.7783)(406)} + \frac{1-0.6121}{(0.6121)(232)} + \frac{1-0.2613}{(0.2613)(111)} \right]$$

$$= 0.000258$$

Now the standard error is calculated by taking the square root of the variance.

$$\text{Standard error} = 0.000258^{-2}$$

$$= 0.16062$$

$$\text{Two standard errors} = 0.032125$$

Therefore, the probability of this sequence occurring during the breeding season is = 0.0979 ± 0.032125 (2 SE).

Appendix VIII. The calculations for the probability and standard error of the five-behavior sequence with the highest probability of occurrence for the younger adult male walrus during the breeding season.

Using the values in the transition probability matrix (Table 16), the probabilities for transitions between behaviors 2 (up) and 5 (sink), 5 (sink) and 9 (whine), 9 (whine) and 4 (float), 4 (float) and 3 (dive), and finally 3 (dive) and 2 (up) were multiplied together to determine the probability of the sequence "up-sink-whine-float-dive-up".

$$\underset{\#2\text{-}5}{(0.5852)}\underset{\#5\text{-}9}{(0.1227)}\underset{\#9\text{-}4}{(0.7121)}\underset{\#4\text{-}3}{(0.5621)}\underset{\#3\text{-}2}{(0.8215)} = 0.0236$$

Now using the probability of the sequence (0.0236), the transition probabilities that were used in the above equation, and the total number of times that the first behavior in each of the transitions was observed (the sum of the rows in Table 12), the variance of this probability can be calculated.

$$\text{Variance} = (0.0236)^2 \left[\frac{1-0.5852}{(0.5852)(1097)} + \frac{1-0.1227}{(0.1227)(717)} + \frac{1-0.7121}{(0.7121)(132)} + \frac{1-0.5621}{(0.5621)(354)} + \frac{1-0.8215}{(0.8215)(325)} \right]$$

$$= 9.09 \times 10^{-6}$$

Now the standard error is calculated by taking the square root of the variance.

$$\text{Standard error} = (9.09 \times 10^{-6})^{-2}$$

$$= 0.0030$$

$$\text{Two standard errors} = 0.0060$$

Therefore, the probability of this sequence occurring during the breeding season is = 0.0236 ± 0.0060 (2 SE).

Appendix IX. The calculations for the probability and standard error, outside the breeding season, of the five-behavior sequence with the highest probability of occurrence for the older male walrus during the breeding season.

Using the values in the transition probability matrix (Table 15), the probabilities for transitions between behaviors 2 (up) and 4 (dive), 4 (dive) and 1 (surface), 1 (surface) and 3 (rest), 3 (rest) and 5 (float), and finally 5 (float) and 2 (up) were multiplied together to determine the probability of the sequence "up-dive-surface-rest-float-up".

$$\underset{\#2\text{-}4}{(0.1304)}\underset{\#4\text{-}1}{(0.3133)}\underset{\#1\text{-}3}{(0.0408)}\underset{\#3\text{-}5}{(0.1875)}\underset{\#5\text{-}2}{(0.0273)} = 8.53 \times 10^{-6}$$

Now using the probability of the sequence (8.53×10^{-6}), the transition probabilities that were used in the above equation, and the total number of times that the first behavior in each of the transitions was observed (the sum of the rows in Table 12), the variance of this probability can be calculated.

$$\text{Variance} = (8.53 \times 10^{-6})^2 \left[\frac{1-0.1304}{(0.1304)(23)} + \frac{1-0.3133}{(0.3133)(83)} + \frac{1-0.0408}{(0.0408)(49)} + \frac{1-0.1875}{(0.1875)(32)} + \frac{1-0.0273}{(0.0273)(110)} \right]$$

$$= 9.1349 \times 10^{-11}$$

Now the standard error is calculated by taking the square root of the variance.

$$\text{Standard error} = (9.1349 \times 10^{-11})^{-2}$$

$$= 9.5577 \times 10^{-6}$$

$$\text{Two standard errors} = 1.9115 \times 10^{-5}$$

Therefore, the probability of this sequence occurring during the breeding season is $= 8.53 \times 10^{-6} \pm 1.9115 \times 10^{-5}$ (2 SE).

Appendix X. The calculations for the probability and standard error, outside the breeding season, of the five-behavior sequence with the highest probability of occurrence for the younger male walrus during the breeding season.

Using the values in the transition probability matrix (Table 15), the probabilities for transitions between behaviors 2 (up) and 5 (sink), 5 (sink) and 9 (whine), 9 (whine) and 4 (float), 4 (float) and 3 (dive), and finally 3 (dive) and 2 (up) were multiplied together to determine the probability of the sequence "up-sink-whine-float-dive-up".

$$(0.3661)(0.0359)(\ 0\ )(0.1176)(0.3235) = 0$$
$$\#2\text{-}5 \quad \#5\text{-}9 \quad \#9\text{-}4 \quad \#4\text{-}3 \quad \#3\text{-}2$$

Therefore, this sequence never occurred outside the breeding season for the younger adult male.

Appendix XI. The calculations for the probability and standard error of the five-behavior sequence with the highest probability of occurrence for the older adult male walrus during the breeding season, from observations made through the underwater windows.

Using the values in the transition probability matrix (Table 17), the probabilities for transitions between behaviors 2 (up) and 4 (dive), 4 (dive) and 1 (surface), 1 (surface) and 3 (rest), 3 (rest) and 5 (float), and finally 5 (float) and 2 (up) were multiplied together to determine the probability of the sequence "up-dive-surface-rest-float-up".

$$(0.7829)(0.7723)(0.6656)(0.7114)(0.1495) = 0.0428$$
$$\#2\text{-}4 \quad \#4\text{-}1 \quad \#1\text{-}3 \quad \#3\text{-}5 \quad \#5\text{-}2$$

Now using the probability of the sequence (0.0428), the transition probabilities that were used in the above equation. and the total number of times that the first behavior in each of the transitions was observed (the sum of the rows in Table 14), the variance of this probability can be calculated.

$$\text{Variance} = (0.0428)^2 \left[\frac{1-0.7829}{(0.7829)(350)} + \frac{1-0.7723}{(0.7723)(483)} + \frac{1-0.6656}{(0.6656)(640)} + \frac{1-0.7114}{(0.7114)(402)} + \frac{1-0.1495}{(0.1495)(368)} \right]$$

$$= 4.41 \times 10^{-5}$$

Now the standard error is calculated by taking the square root of the variance.

$$\text{Standard error} = (4.41 \times 10^{-5})^{-2}$$

$$= 0.0066426$$

$$\text{Two standard errors} = 0.0133$$

Therefore, the probability of this sequence occurring during the breeding season is = 0.0428 ± 0.0133 (2 SE).

Appendix XII. The calculations for the probability and standard error of the five-behavior sequence with the highest probability of occurrence for the younger adult male walrus during the breeding season. from observations made through the underwater windows.

Using the values in the transition probability matrix (Table 17), the probabilities for transitions between behaviors 2 (up) and 5 (sink), 5 (sink) and 7 (bell), 7 (bell) and 1 (surface), 1 (surface) and 4 (float), and finally 4 (float) and 2 (up) were multiplied together to determine the probability of the sequence "up-sink-bell-surface-float-up".

$$(0.5033)(0.6400)(0.2168)(0.9140)(0.5958) = 0.0380$$
$$\#2\text{-}5 \quad \#5\text{-}7 \quad \#7\text{-}1 \quad \#1\text{-}4 \quad \#4\text{-}2$$

Now using the probability of the sequence (0.0380), the transition probabilities that were used in the above equation, and the total number of times that the first behavior in each of the transitions was observed (the sum of the rows in Table 14), the variance of this probability can be calculated.

$$\text{Variance} = (0.0380)^2 \left[\frac{1-0.5033}{(0.5033)(1383)} + \frac{1-0.6400}{(0.6400)(725)} + \frac{1-0.2168}{(0.2168)(452)} + \frac{1-0.9140}{(0.9140)(93)} + \frac{1-0.5958}{(0.5958)(523)} \right]$$

$$= 1.704 \times 10^{-5}$$

Now the standard error is calculated by taking the square root of the variance.

$$\text{Standard error} = (1.704 \times 10^{-5})^{-2}$$

$$= 0.00304$$

$$\text{Two standard errors} = 0.0061$$

Therefore, the probability of this sequence occurring during the breeding season is = 0.0380 ± 0.0061 (2 SE).

Appendix XIII. The calculations for the probability and standard error of the three-behavior sequence with the highest probability of occurrence for the younger adult male walrus during the breeding season, from observations made through the underwater windows.

Using the values in the transition probability matrix (Table 17), the probabilities for transitions between behaviors 2 (up) and 5 (sink), 5 (sink) and 7 (bell), and 7 (bell) and 2 (up) were multiplied together to determine the probability of the sequence "up-sink-bell-up".

$$(0.5033)(0.6400)(0.6173) = 0.1988$$
$$\#2\text{-}5 \quad \#5\text{-}7 \quad \#7\text{-}2$$

Now using the probability of the sequence (0.1988), the transition probabilities that were used in the above equation. and the total number of times that the first behavior in each of the transitions was observed (the sum of the rows in Table 14), the variance of this probability can be calculated.

$$\text{Variance} = (0.1988)^2 \left[\frac{1-0.5033}{(0.5033)(1383)} + \frac{1-0.6400}{(0.6400)(725)} + \frac{1-0.6173}{(0.6173)(452)} \right]$$

$$= 1.113 \times 10^{-4}$$

Now the standard error is calculated by taking the square root of the variance.

$$\text{Standard error} = (1.113 \times 10^{-4})^{-2}$$

$$= 0.0106$$

$$\text{Two standard errors} = 0.0213$$

Therefore, the probability of this sequence occurring during the breeding season is = 0.1988 ± 0.0213 (2 SE).

Appendix XIV. The calculations for the probability and standard error the three-behavior sequence with the second highest probability of occurrence for the younger adult male walrus during the breeding season, from observations made through the underwater windows.

Using the values in the transition probability matrix (Table 17), the probabilities for transitions between behaviors 2 (up) and 6 (splash), 6 (splash) and 3 (dive), and 3 (dive) and 2 (up) were multiplied together to determine the probability of the sequence "up-splash-dive-up".

$$(0.1280)(0.9076)(0.7417) = 0.0862$$
$$\#2\text{-}6 \quad \#6\text{-}3 \quad \#3\text{-}2$$

Now using the probability of the sequence (0.0862), the transition probabilities that were used in the above equation, and the total number of times that the first behavior in each of the transitions was observed (the sum of the rows in Table 14), the variance of this probability can be calculated.

$$\text{Variance} = (0.0862)^2 \left[\frac{1-0.1280}{(0.1280)(1383)} + \frac{1-0.9076}{(0.9076)(184)} + \frac{1-0.7417}{(0.7417)(360)} \right]$$

$$= 4.8 \times 10^{-5}$$

Now the standard error is calculated by taking the square root of the variance.

$$\text{Standard error} = (4.8 \times 10^{-5})^{-2}$$

$$= 0.0069$$

$$\text{Two standard errors} = 0.0138$$

Therefore, the probability of this sequence occurring during the breeding season is = 0.0862 ± 0.0138 (2 SE).

LITERATURE CITED

Allen, J. A. 1880. History of North American Pinnipeds: A Monograph of the Walruses, Sea-lions, Sea-bears and Seals of North America. U. S. Geol. Geogr. Surv. Terr., Misc. Publ. 12. 785 pp.

Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. Evolution 24:546-559.

Bartholomew, G. A. and N. E. Collias. 1962. The role of vocalization in the social behavior of the northern elephant seal. Anim. Behav. 10:7-14.

Bartholomew, G. A. and P. G. Hoel. 1953. Reproductive behaviour in the Alaska fur seal. Callorhinus ursinus. J. Mammal. 34(4):417-436.

Bel'kovich, V. M. and A. V. Yablokov. 1961. Among the walruses. Priroda (Moscow) 1961(3):50-56.

Bonner, W. N. 1981. Grey Seal - Halichoerus grypus. In: R. J. Harrison and S. H. Ridgway (eds.). Handbook of Marine Mammals, Volume 2, pp. 111-144. Academic Press, New York. 359 pp.

Bridges, W. 1953. The weighing of Herbert. Anim. Kingdom 56(1):19-21.

Brody, S. 1945. Bioenergetics and Growth. Reinhold Publishing Corp., New York. 1023 pp.

Brooks, J. W. 1954. A contribution to the life history and ecology of the Pacific walrus. Alaska Cooperative Wildlife Research Unit, University of Alaska, Fairbanks, Spec. Rep. 1. 103 pp.

Brown, D. H. and E. D. Asper. 1966. Further observations on the diet and growth of the Pacific walrus, (Odobenus rosmarus divergens), in captivity. Int. Zoo Yearbook 6:78-81.

Burns, J. J. 1965. The walrus in Alaska, its ecology and management. Alaska Dept. Fish and Game. Juneau. 48 pp.

Burns, J. J. 1967. The Pacific bearded seal. Alaska Department of Fish and Game, Juneau. 66 pp.

Burns, J. J. 1970. Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi seas. J. Mammal. 51:445-454.

Burns, J. J. and K. J. Frost. 1979. The natural history and ecology

of the bearded seal, Erignathus barbatus. Alaska Dept. of Fish and Game, Fairbanks. 77 pp.

Chapskii, K. K. 1936. The walrus of the Kara Sea. Trudy Vsesoiuz. Arkt. Inst. (Leningrad) 67:1-124.

Christenson, T. E. and B. J. Le Boeuf. 1978. Aggression in the female northern elephant seal Mirounga angusirostris. Behaviour 64:158-172.

Cline, D. R., D. B. Siniff, and A. Q. Erickson. 1971. Underwater copulation of the Weddell seal. J. Mammal. 52:216-218.

Collins, G. 1940. Habits of the Pacific walrus (Odobaenus divergens). J. Mammal. 21:138-144.

Conover, W. J. 1980. Practical Nonparametric Statistics. Second Edition. John Wiley and Sons, New York. 493 pp.

Eley, T. J. 1978. A possible case of adoption in the Pacific walrus. Murrelet 59:77-78.

Fay, F. H. 1960. Structure and function of the pharyngeal pouches of the walrus (Odobenus rosmarus, Linnaeus). Mammalia 24:361-371.

Fay, F. H. 1982. Ecology and biology of the Pacific walrus. North American Fauna 74. U. S. Fish and Wildlife Service, Washington. 279 pp.

Fay, F. H. and B. P. Kelly. 1980. Mass natural mortality of walruses (Odobenus rosmarus) at St. Lawrence Island, Bering Sea, autumn 1978. Arctic 33:226-245.

Fay, F. H. and G. C. Ray. 1968. Influence of climate on the distribution of walruses Odobenus rosmarus (Linnaeus). I. Evidence from thermoregulatory behavior. Zoologica 53:1-18.

Fay, F. H. and G. C. Ray. 1979. Reproductive behavior of the Pacific walrus in relation to population structure. In: B. R. Melteff (ed.) Alaska Fisheries: 200 Years and 200 Miles of Change. pp. 409-410. Proc. 29th Alaska Science Conf. 1978. Sea Grant Program, Univ. of Alaska, Fairbanks.

Fay, F. H., G. C. Ray, and A. A. Kibal'chich. 1984. Time and location of mating and associated behavior of the Pacific walrus Odobenus rosmarus divergens, Illiger. In: F. H. Fay and G. A. Fedoseev (eds.), Soviet-American Cooperative Research on Marine Mammals, Vol. 1, Pinnipeds. NOAA. National Marine Fisheries Service Technical Report. In Press.

Fedak, M. A. and S. S. Anderson. 1982. The energetics of lactation: accurate masurements from a large wild mammal, the grey seal (Halichoerus grypus). J. Zool. (London) 198:473-479.

Fedoseev, G. A. 1976. Giants of the polar seas. Priroda (Moscow) 1976(8):76-83.

Fogden, S. C. L. 1968. Suckling behavior in the grey seal (Halichoerus grypus) and the northern elephant seal (Mirounga angustirostris). J. Zool. (London) 154:415-420.

Fogden, S. C. L. 1971. Mother-young behaviour at grey seal breeding beaches. J. Zool. (London) 164:61-92.

Geraci, J. R. 1975. Pinniped nutrition. Rapp. P.-v. Reun. Cons. int. Explor. Mer 169:312-323.

Gove, P. B. 1976. Webster's Third New International Dictionary of the English Language, Unabridged. G. and C. Merriam Company, Springfield, Massachusetts. 2662 pp.

Hagenbeck, G. H. 1963. Notes on walruses, Odobenus rosmarus, in captivity. Int. Zoo Yearbook 4:24-25.

Harrison, R. J. 1969. Reproduction and reproductive organs. In: H. T. Andersen (ed.), The Biology of Marine Mammals, pp. 253-348. Academic Press, New York.

Heinrich, A. 1947. Their friend the walrus. (Unpubl. manuscript)

Hinde, R. A. 1974. The course of rhesus mother-infant interaction. In: R. A. Hinde (ed.), Biological Bases of Human Social Behavior, pp. 193-208. McGraw-Hill, New York.

Hiller, F. S. and G. J. Lieberman. 1967. Operations Research. Second Edition. Holden - Day, Inc. 800 pp.

Kleiber, M. 1961. The Fire of Life: An Introduction to Animal Energetics. John Wiley and Sons, New York. 454 pp.

Kooyman, G. L. 1968. An analysis of some behavioural and physiological characteristics related to diving in the Weddell seal. Antarctic Res. Ser. 11:227-261.

Le Boeuf, B. J., R. J. Witing, and R. F. Gantt. 1972. Perinatal behavior of northern elephant seal females and their young. Behaviour 43:121-156.

Ling, J. K . and M. M. Bryden. 1981. Southern elephant seal, Mirounga leonina. In: R. J. Harrison and S. H. Ridgeway (eds.).

Handbook of Marine Mammals, Volume 2, pp. 297-328. Academic Press, New York. 359 pp.

Loughrey, A. G. 1959. Preliminary investigation of the Atlantic walrus Odobenus rosmarus rosmarus (Linnaeus). Can. Wildl. Serv., Wildl. Manage. Bull. 14, Ser. 1. 123 pp.

Mansfield, A. W. 1958a. The biology of the Atlantic walrus Odobenus rosmarus rosmarus (Linnaeus) in the eastern Canadian arctic. Fish. Res. Bd. Can. Manuscr. Rep. Ser. (Biol.) 653. 146 pp.

Mansfield, A. W. 1958b. The breeding behavior and reproductive cycle of the Weddell seal (Leptonychotes weddelli Lesson). Falkland Islands Depend. Surv. Sci. Rep. 18. 41 pp.

Mansfield, A. W. 1967. Seals of arctic and eastern Canada. Fish. Res. Bd. Can. Bull. 137:1-36.

McCullogh, B. 1974. Walrus study 1974 - Coats Island, N. W. T. Unpubl. Rep., Fisheries Research Board Canada, Montreal. 5 pp.

McLaren, I. A. 1958. The biology of the ringed seal (Phoca hispida Schreber) in the eastern Canadian Arctic. Fish. Res. Bd. Can. Bull., 118:1-97.

Merdsoy, B. R., W. R. Curtsinger, and D. Renouf. 1978. Preliminary underwater observations of the breeding behavior of the harp seal (Pagophilus groenlandicus). J. Mammal. 59:181-185.

Miller, E. H. 1975a. A comparative study of facial expressions of two species of pinnipeds. Behaviour 53:268-284.

Miller, E. H. 1975b. Walrus ethology: I. The social role of tusks and applications of multidimensional scaling. Can. J. Zool. 53:590-613.

Miller, E. H. 1976. Walrus ethology: II. Herd structure and activity budgets of summering males. Can. J. Zool. 54:704-715.

Miller, E. H. 1982. Herd organisation and female threat behavior in Atlantic walruses Odobenus rosmarus rosmarus (L.). Mammalia 46:29-34.

Miller, E. H. and D. J. Boness. 1983. Summer behavior of Atlantic walruses Odobenus rosmarus rosmarus (Linnaeus) at Coats Island, N. W. T. (Canada). Z. Saugetierk. 48:298-313.

Nikulin, P. G. 1941. The Chukchi walrus. Izv. TINRO (Vladivostok) 20:21-59.

Pederson, A. 1962. Das Walross. Die neue Brehm-Bucherie, Heft 306. A. Ziemsen, Wittenberg. 60 pp.

Peterson, R. S. and G. A. Bartholomew. 1967. The natural history and behavior of the California sea lion. Spec. Publ. #1, American Society of Mammalogists.

Petrinovich, L. 1974. Individual recognition of pup vocalization by northern elephant seal mothers. Z. Tierpsychol. 34:308-312.

Pike, R. L. and M. L. Brown. 1975. Nutrition: An Integrated Approach. Second Edition. John Wiley and Sons Inc., New York. 1082 pp.

Popov, L. A., A. A. Kibal'chich, Yu. A. Bukhtiyarov, and M. V. Yurakhno. 1981. Materials from investigation of pinnipeds during the expedition on the Z.R.S. Zvyagino in the Bering Sea, February - March 1981, pp. 38-54. In Popov, L. A. (ed.), Scientific investigational work on marine mammals in the northern part of the Pacific ocean 1980-81. All-Union Scientific Investigational Institute of Marine Fisheries and Oceanography (VNIRO), Moscow.

Ray, G. C. 1967. Social behavior and acoustics of the Weddell seal. Antarctic J. U. S. 2:105-106.

Ray, G. C. and W. A. Watkins. 1975. Social function of underwater sounds in the walrus Odobenus rosmarus. In: K. Ronald and A. W. Mansfield (eds.), Biology of the Seal, Rapp. P.-v. Reun. Cons. int. Explor. Mer 169:524-526.

Ray, G. C., W. A. Watkins, and J. J. Burns. 1969. The underwater song of Erignathus (bearded seal). Zoologica 54:79-83.

Reventlow, A. 1951. Observations on the walrus (Odobenus rosmarus) in captivity. Zool. Gart. (N. F.) 18:227-234.

Russell, E. 1976. The birth of a walrus in a controlled environment. Unpubl. Rep., Moorpark College, California. 39 pp.

Salter, R. E. 1978. Normal behavior and disturbance responses of walruses (Odobenus rosmarus, Linnaeus) during terrestrial haul-out, eastern Bathurst Island, N. W. T., July - August 1977. Polar Gas Project, LGL Ltd., Toronto. Canada. 68 pp.

Salter, R. E. 1979. Site utilization, activity budgets and disturbance responses of Atlantic walruses during terrestrial haul-out. Can. J. Zool. 57:1169-1180.

Salter, R. E. 1980. Observations on social behaviour of Atlantic walruses (Odobenus rosmarus (L.)) during terrestrial haul-out.

Can. J. Zool. 58:461-463.

Sandegren, F. E. 1970. Breeding and maternal behavior of the Steller sea lion (Eumetopias jubata) in Alaska. Unpubl. M. S. Thesis. University of Alaska, Fairbanks, Ak. 138 pp.

Schevill, W. E. and W. A. Watkins. 1971. Directionality of the sound beam in Leptonychotes weddelli (Mammalia:Pinnipedia). Antarctic Res. Ser. 18:163-168.

Schevill, W. R., W. A. Watkins, and G. C. Ray. 1966. Analysis of underwater Odobenus calls with remarks on the development of the pharyngeal pouches. Zoologica 51:103-106.

Slater, P. J. B. and N. P. Lester. 1982. Minimizing errors in splitting behaviour into bouts. Behaviour 79:153-161.

Smith, M. S. R. 1966. Injuries as an indication of social behaviour in the Weddell seal (Leptonychotes weddelli). Mammalia 30:241-246.

Spalding, D. J. 1964. Comparative feeding of the fur seal, sea lion, and harbor seal on the British Columbia coast. Fish. Res. Bd. Can. Bull. 146:1-52.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51:3-47.

Stirling, I. and R. M. Warneke. 1971. Implications of a comparison of the airborne vocalizations and some aspects of the behavior of the two Australian fur seal species (Arctocephalus, sp.) on the evoluation and present taxonomy of the genus. Australian J. Zool. 19:227-242.

Stirling, I., H. Cleator, and W. Calvert. 1982. Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the high arctic. Report prepared for Arctic Pilot Project, Dome Petroleum Limited, Esso Resources Canada Limited. 54 pp.

Taber, S. and P. Thomas. 1982. Mother-calf spacing in right whales. Anim. Behav. 30:1072-1083.

Tinbergen, N. 1952. "Derived" activities; their causation, biological significance, origin, and emancipation during evolution. Quart. Rev. Biol. 27:1-32.

Venables, U. M. and L. S. V. Venables. 1957. Mating behaviour of the seal Phoca vitulina in Shetland. Proc. Zool. Soc. Lond. 128:387-396.

Watkins, W. A. and W. E. Schevill. 1968. Underwater playback of their own sounds to Leptonychotes (Weddell seals). J. Mammal. 49:287-296.

Wilson, S. 1974. Mother-young interactions in the common seal, Phoca vitulina vitulina. Behaviour 48:23-36.

Zabel, C., J. Taggart, and B. P. Kelly. 1982. Behavior studies of a mixed herd of Pacific walruses. Unpublished Manuscript. 28 pp.

Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 620 pp.